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Jorde, K.

STREAM ECOSYSTEM RESPONSE TO WILDFIRE

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Final Report

Joint venture agreement between:
USDA Forest Service, Rocky Mountain Research Station
Agreement Number: 02-JV-11222014-196
and

University of Idaho
Project number: FKK493
Prepared by:

Klaus Jorde, Amanda E. Rosenberger, Nicholas E. Scheidt, Chris W. Welcker

University of Idaho
Center for Ecohydraulics Research
Department of Civil Engineering
Idaho Water Center, 322 E. Front St.
Boise, ID 83702

Bruce E. Rieman (retired), Charles H. Luce,
John M. Buffington, James A. McKean
US Forest Service, Rocky Mountain Research Station
Idaho Water Center, 322 E. Front St.
Boise, ID 83702

Jason B. Dunham
USGS FRESC Corvallis Research Group
3200 SW Jefferson Way
Corvallis, OR 97331

RMRS Library
USDA Forest Service
OCT 2 3 2007
240 W Prospect Rd
Fort Collins CO 80526

With Contributions by:

Erica A. Swenson
Biology Department, Albertson College of Idaho
2112 Cleveland Boulevard, Caldwell, Idaho 83605

Philip Howell
U.S. Department of Agriculture- Forest Service
Forestry and Range Sciences Laboratory
1401 Gekeler Lane, La Grande, Oregon 97850

Reporting Period: January 1, 2006 – June 23, 2007

PURPOSE

The purpose of this agreement is to quantify the influence that large wildfires and subsequent modification of watershed processes may have on aquatic ecosystems and the persistence of sensitive aquatic species. Because the effects of wildfire may be highly variable, research contained in this project is focused on fires and subsequent disturbances that are most disruptive to aquatic ecosystems. Efforts were concentrated on watersheds that had stand replacing fire followed by channel reorganization due to debris flows, hyperconcentrated flows, and/or floods. The work done under this agreement focused on three general areas: 1) effects of fire-related debris flows and hyperconcentrated flows on channel morphology and aquatic habitat; 2) successional changes in channel morphology over time following fire disturbance; and 3) effects of fire and ecological context on aquatic biological diversity. The following report is divided into sections for each of the three research areas, and describes how objectives were achieved as stated in the project workplan.

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PROJECT ACCOMPLISHMENTS

Peer-reviewed publications

Swenson, E.A., A.E. Rosenberger, and P.J. Howell. 2007. Validation of endoscopy for non-lethal determination of maturity of small brook trout. Transactions of the American Fisheries Society 136:994-998.

Dunham, J.B., A.E. Rosenberger, C.H. Luce, and B.E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. Ecosystems 10:335-346.

Dunham, J., G. Chandler, B.E. Rieman, and D. Martin. 2005. Measuring stream temperature with digital data loggers: A user's guide. General Technical Report. RMRS-GTR-150WWW. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 15 pp.

Rosenberger, A.E. and J.B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395–1410.

Publications in prep.

Rosenberger, A.E., J.B. Dunham, T. Copeland, and B.E. Rieman. in prep. Population and life history response of rainbow trout Onchorynchus mykiss to severe wildfire and channel reorganization in Central Idaho headwater streams. Ecological Applications.

Neville, H., A.E. Rosenberger, and J.B. Dunham. in prep. Landscape genetic responses of rainbow trout (*Oncorhynchus mykiss*) to channel disturbance and wildfire in Idaho river basins. Ecological Applications.

Dunham, J.B., A.E. Rosenberger, R.F. Thurow, A. Dolloff, and P.J. Howell. in prep. Coldwater fishes in wadeable streams. In. S. Bonar, W. Hubert, and D. Willis, editors. Standard Sampling Methods for North American Freshwater Fishes. American Fisheries Society, Fisheries Management Section.

Rosenberger, A.E., J.B. Dunham, M.S. Wipfli, and J.M. Buffington. in prep. Effects of wildfire and channel reorganization on drifting macroinvertebrates and predation by trout in central Idaho streams a decade after disturbance. Transactions of the American Fisheries Society.

Student theses/dissertations

Scheidt, N.E. Stream succession: channel changes after wildfire disturbance. 2006. unpub. M.S. thesis. Department of Civil Engineering, University of Idaho, Boise, ID, 60 pp.

Presentations to scientific organizations (published abstracts & proceedings)

Rosenberger, A.E., J.B. Dunham, H. Neville, and B.E. Rieman. Resilience of rainbow trout in Idaho streams to wildfire-related disturbance. 2006. Annual meeting of American Fisheries Society, Lake Placid, New York.

Dunham, J.B., J.M. Buffington, B. Gutierrez, C.H. Luce, D. Nagel, B.E. Rieman, and A.E. Rosenberger. 2005. Effects of wildfire on fish populations: contemporary changes and long-term consequences. Climate and Fisheries: Impacts, Uncertainty, and Responses of Ecosystems and Communities. Victoria, British Columbia, October 26-28, 2005.

Dunham, J.B., C.H. Luce, A.E. Rosenberger, B. Gutiérrez Teira, D. Nagel, and B.E. Rieman. 2005. Wildfire, channel disturbance, and stream temperature: spatio-temporal patterns and

associations with the distribution of fish and amphibians in central Idaho. EOS, Transactions, American Geophysical Union 86(18):Joint Assembly Supplement, Abstract B42A-06.

Rieman, B., J. Dunham, C. Luce, and A. Rosenberger. 2005. Implications of changing fire regimes for aquatic ecosystems. In Taylor, L., J. Zelnik, S. Cadwallader, and Hughes (editors), Mixed Severity Fire Regimes: Ecology and Management, 187-191. Symposium Proceedings, Spokane WA. November 15-19, 2004. Washington State University, Pullman, WA. **(Invited)**

Rosenberger, A.E. and J.B. Dunham. 2005. Validation of abundance estimates from mark recapture and removal techniques for rainbow trout captured by electrofishing in small streams. Annual meeting of the American Fisheries Society, Anchorage, AK.

Rosenberger, A.E., J.B. Dunham, and B.E. Rieman. 2005. The effects of wildfire and channel disturbance on individual and life-history traits of rainbow trout in Idaho streams. Annual meeting of the American Fisheries Society, Anchorage, AK.

Rosenberger, A.E., J.B. Dunham, M.S. Wipfli, and J.M. Buffington. 2005. Effects of fire and subsequent channel-reorganizing events on invertebrate drift and rainbow trout diet in small headwater streams 10 years post-disturbance. EOS, Transactions American Geophysical Union 86(18):Joint Assembly Supplement, Abstract B43B-03.

Welcker, C.W., J.M. Buffington, C.H. Luce, and J. McKean. 2005. The potential influence of stair-step morphology on the initiation of bulking debris flows in southwestern Idaho, USA, 4 Geological Society of America Abstracts with Programs, 37(7):35. Annual Meeting, Salt Lake City, UT, October 16-19, 2005. **(Invited)**

Welcker, C.W., J.M. Buffington, C.H. Luce, B.E. Rieman, and J. McKean. 2005. Long-term impacts of fire and mass wasting on solar loading and stream heating in mountain streams of central Idaho, EOS, Transactions of the American Geophysical Union, 86(52):Fall Meeting Supplement, Abstract H13K-04.

Buffington, J.M., N.E. Scheidt, and C.W. Welcker. 2004. Channel geometry of mountain rivers within the debris-flow process domain of the Idaho Batholith. EOS, Transactions American Geophysical Union, 85(47):Fall Meeting Supplement, Abstract H41G-01.

Scheidt, N.E., C.H. Luce, J.M. Buffington, B.E. Rieman, and T.A. Black. 2004. Stream succession: channel changes after wildfire disturbance. EOS, Transactions American Geophysical Union, 85(47):Fall Meeting Supplement, Abstract H53C-1270.

Welcker, C.W., J.M. Buffington, B.E. Rieman, C.H. Luce, and J. McKean. 2004. Impacts of fire and mass wasting on channel morphology and stream temperature in mountain rivers of central Idaho. EOS Transactions, American Geophysical Union, 85(47):Fall Meeting Supplement, Abstract H53C-1271.

Rosenberger, A.E., J.B. Dunham, and B.E. Rieman. 2003. Evaluating watershed vulnerability: a fish perspective on fire. Geological Society of America Conference on Wildland Fire Impacts on Watersheds: Understanding, Planning and Response, Denver, CO.

Lectures, workshops, short courses

Rosenberger, A.E., J.B. Dunham, H. Neville, and B.E. Rieman. 2006-7. Resilience of rainbow trout in Idaho streams to wildfire-related disturbance. Presented at:

- Freshwater Ecosystems Seminar Series, University of Alaska, Fairbanks School of Fisheries and Ocean Sciences.
- Fisheries Seminar Series, University of Alaska Fairbanks, Juneau Center.
- Seminar, Alaska Department of Fish and Game Operational Planning Meeting.

Rosenberger, A.E., J.B. Dunham, B.E. Rieman, M.S. Wipfli, and J.M. Buffington. 2006. Wildfire and recovery of salmonid populations: a case study of the Boise River Basin. Presented at:

- US Forest Service, Region 4, Integrated Resources Workshop, Ogden, UT, March 27-31, 2006.
- Seminar, Department of Forest, Range, and Wildlife Resources, Utah State University, Logan, UT.

Rosenberger, A.E., R.F. Thurow, J.B. Dunham, and J. Peterson. 2006. Utility of electrofishing and snorkeling for censusing salmonids: why validation is essential. Presented at:

- Seminar, Joint Bonnevile and Colorado River Cutthroat Trout Meeting, Salt Lake City, UT
- US Forest Service, Region 4, Integrated Resources Workshop, Ogden, UT, March 27-31, 2006.

Rosenberger, A.E., J.B. Dunham, M.S. Wipfli, J.M. Buffington, and B.E. Rieman, 2005. Fire, channel reorganization, and aquatic vertebrate response: Emphasis on rainbow trout food base and diet. Colloquium. Department of Geosciences, Idaho State University. Pocatello, ID. April 13, 2005 **(Invited)**

Luce, C.H., B.E. Rieman, J.B. Dunham, and J.M. Buffington. 2004/5. Short course. Fire, watershed processes and aquatic ecosystems. Presented at:

- Advancing the Fundamental Sciences—A Conference for Forest Service Physical Scientists, San Diego, CA, October 18-22, 2004. **(Invited)**
- Region 4 Integrated Resource Workshop, Working Towards Healthy Forests, Ogden, UT, April 11-14, 2005.
- Boise National Forest, Boise, ID, April 19, 2005. **(Invited)**

Dunham, J., C. Luce, B. Rieman, and A. Rosenberger. 2004. How does severe wildfire and extreme disturbance affect fish? Seminar presented to the College of Natural Resources, Utah State University, Logan, UT. **(Invited)**

Dunham, J.B., A.E. Rosenberger, and B.E. Rieman. 2004. Fire and fish. Presentation to visiting foresters from Tomsk, Russia, hosted by the National Interagency Fire Center, Boise, ID.

Dunham, J.B., A.E. Rosenberger, B.E. Rieman, and C.H. Luce. 2004. Effects of fire on fish populations: looking from genes to ecosystems. Seminar presented to USGS Forest and Rangeland Ecosystem Science Center and Oregon State University, Corvallis, OR.

RESEARCH AREA 1: EFFECTS OF FIRE-RELATED DEBRIS FLOWS AND HYPERCONCENTRATED FLOWS ON CHANNEL MORPHOLOGY AND AQUATIC HABITAT

Ph.D. research of
Chris W. Welcker

INTRODUCTION

Post-fire channel disturbances due to debris flows, hyperconcentrated flows, and floods can significantly alter channel characteristics and aquatic habitat in mountain basins. These disturbances are collectively termed channel-reorganizing events. Debris flows and hyperconcentrated flows are the most common post-fire disturbances observed in the Idaho batholith, and a single mass wasting event can exhibit both styles of flow (debris vs. hyperconcentrated) due to changes in valley slope, flow depth, and incorporation or expulsion of water and sediment as the disturbance moves down valley. Consequently, we combine these two mass wasting rheologies into a single category of debris/hyperconcentrated flows (D/HFs).

The purpose of this study was to: 1) quantify the D/HF process domain (Montgomery 1999) and the characteristics of D/HFs in the Idaho batholith; 2) describe the influence of D/HFs on fish habitat, especially with regard to stream temperatures; 3) characterize the evolution of these D/HF impacts through time; and 4) create an assessment tool to identify channels impacted by D/HFs and to estimate the date of disturbance. Objective 4 has been abandoned because of complexities beyond the intended scope of work, and because a more thorough, longer-term study does not suit the RMRS's needs at this time. A new objective, 5, was added (see Jorde et. al. 2005 for a full description) which examines the hillside initiation zones of D/HFs. The overall intent of these investigations is to examine the immediate and long-term impacts of fire and the subsequent D/HFs on aquatic ecosystems.

OVERVIEW OF WORK COMPLETED

The 2003 field season was focused on surveying streams to determine if differences between D/HF-impacted and unimpacted streams were measurable through simple stream surveys. Over 11,000 m were surveyed on 6 different streams. This was also a chance to assess the feasibility of tree coring and lichenometry as dating techniques for assessing recency of D/HFs, Objective 4. Most importantly, it provided a chance to look at D/HF-impacted streams throughout the study area to develop a qualitative sense of the important processes and patterns.

The 2004 field season focused on a quantitative comparison of stream reaches to examine the impacts of D/HFs on stream temperature. Thirty two stream reaches of different disturbance categories and ages of disturbance were surveyed. In the fall of 2004, a second field campaign was undertaken to survey debris-flow gullies from the valley bottom to the ridgeline at 10 hillsides, in support of Objective 5.

During the summer of 2005, five streams from the 2004 survey were reinstrumented and surveyed three times to assess the temporal variability of heat budgets and to quantitatively link the solar loading to stream heating at each site. This will allow us to demonstrate the direct causal relationship between solar radiation and heating for all 32 streams surveyed in 2004.

Results of this work were presented at the 2004 and 2005 American Geophysical Union conferences (Welcker et al. 2004; 2005a). Current efforts are focused on data analysis for all 4 active objectives and preparing manuscripts for publication.

METHODS

Objective 1. Quantify the process domain of debris/hyperconcentrated flows

During fieldwork in 2003, process domains of many D/HFs were identified as beginning on steep, burned or unvegetated hillsides and continuing through the stream network until a critically low slope or confinement is reached, most often at tributary junctions. The susceptibility of a reach of stream to D/HF disturbance is determined by whether an upstream

hillside can initiate a flow and whether the path down to a particular reach is capable of stopping the flow. Because the study area is almost exclusively composed of steep hillsides which can initiate D/HFs, it is the lower bound of the D/HF process domain which delineates the portion of the stream network at risk of D/HF disturbance. This lower bound is expected to be largely determined by the slope and confinement of the reaches (e.g., Whiting and Bradley 1994). Deposition areas and reaches disturbed by D/HFs were surveyed to quantify threshold values of slope and confinement for stopping flows.

Task 1.1. Site Selection

Nine reaches recently disturbed by D/HFs and surveyed as part of Objectives 2 and 3 were selected. Four additional reaches with recent D/HF deposition were chosen to increase the sample size.

Task 1.2. Collect Field Data

Reaches that passed D/HFs and those where deposition occurred were surveyed. Stream slopes and confinement were measured with tape measures and an engineer's level, or with a hand level.

Task 1.3. Data Analysis

A plot of slope versus confinement will be constructed to determine if there is a slope-confinement threshold for D/HF deposition. The threshold should demark a boundary between sites that passed D/HFs versus ones where deposition occurred. This threshold can be applied across the stream network to determine which streams are within the D/HF process domain and at risk of future D/HF disturbance. These data have not been entered or analyzed yet.

Objective 2. Describe the influence of debris/hyperconcentrated flows on fish habitat

Previous work in the study area has shown that stream temperature is one of the main determinants of habitat suitability for salmonids, like the threatened bull trout (Dunham et. al. 2003). While long-term average stream temperatures can be characterized using temporally constant variables like elevation, aspect, drainage area, etc., disturbances such as fire or D/HFs may have significant impacts on the thermal regime of streams. This impact is expected to last for a finite period of time after disturbance before the stream fully recovers, but the length of this time period is unknown. Based on field observations, a conceptual model was developed that describes the way that fire and D/HF disturbance impacts vegetation and, in turn, drives changes to both the stream channel and stream temperature.

Vegetation is divided into 1) a riparian shrub component which directly interacts with the stream channel and 2) a forest canopy component which is more removed from the stream but still provides shade. Riparian vegetation is killed or damaged by the scour and deposition of a D/HF moving through the stream, while canopy forest is largely unaffected. In contrast, fire kills the forest canopy but does less damage to riparian shrubs. The shrubs are partially protected by the cooler, wetter riparian microclimate, and shrubs recover more quickly due to their ability to resprout (Dwire and Kauffman 2003; Noste and Bushey 1987). In fact, riparian shrubs may grow thicker due to the increased sunlight and nutrient availability caused by removal of the canopy.

Solar radiation is expected to be the dominant element of the stream heat budget, and the temperature of the stream is expected to increase with increased solar radiation (Beschta et al.

1987). Thicker riparian vegetation, or the presence of a forest canopy, provides more stream shading leading to cooler temperatures. The removal of riparian vegetation by D/HF disturbance or the removal of trees by fire increases the insolation of the stream and the stream temperature. Moreover, if riparian shrubs are providing cohesion to the stream banks, thicker shrub vegetation will result in more bank cohesion, leading to narrower and deeper channels. Consequently, the removal of riparian vegetation would lessen bank cohesion and lead to wider shallower channels. While the narrower stream channels minimize the exposure of the stream to solar radiation causing it to heat more slowly, the wider, shallower channels and their greater solar exposure lead to increased stream temperatures.

Considering all possible combinations of these disturbances (Fig. 1), leads to the following expectations for vegetation patterns and resultant stream temperatures (in parentheses):

- No Fire & No Debris/Hyperconcentrated Flow: Relatively narrow channel, spotty riparian shrubs, with tree canopy. (Reference temperature)
- No Fire, but Debris/Hyperconcentrated Flow: Wider channel, very little riparian shrub vegetation, with tree canopy. (Warmer)
- Fire & No Debris/Hyperconcentrated Flow: Relatively narrow channel, very thick riparian vegetation, with no tree canopy. (Cooler)
- Fire & Debris/Hyperconcentrated Flow: Wider channel, very little riparian shrub vegetation, with no tree canopy. (Warmer)

During the 2004 field season, we set out to test these conceptual models of vegetation, channel, and stream temperature change after disturbance. Specifically, we tested whether the insolation of the study reaches changed, as predicted, as a function of altered stream width and shading. We also tested whether this altered solar radiation flux to the stream adequately explained the observed changes in stream temperature.

Task 2.1. Site Selection

Clusters of recently impacted sites and controls were chosen to look at the immediate impacts of disturbance on stream temperature and variables related to the solar heating of streams. In the Deadwood River area, we looked at 3 unburned streams impacted by D/HFs that occurred in 2003, and 3 control sites (Fig. 2). In the headwaters of Middle Fork Boise River, we looked at 3 burned sites impacted by D/HFs that occurred in 2004, 3 streams that were burned and undisturbed by D/HFs, and 4 control streams (Fig. 2). Sites were chosen to have similar drainage areas, and to be located close to one another.

Task 2.2. Collect Field Data

Stream temperature was monitored at the top and bottom of 200-600 m reaches during summer 2004 from July through September. The burned and D/HF-disturbed sites were chosen after D/HF disturbances that occurred in 2003, but during the summer of 2004, they experienced two more D/HFs, which removed temperature sensors. This resulted in a short temperature record from late August and September. All reaches were surveyed every 20 m for channel width, depth, vegetation, particle size, and shading. Vegetation was measured as shrub stems per square meter on stream banks. Five valley cross-sections were surveyed for each reach to

measure confinement and examine patterns of shrub abundance. Patterns of solar radiation were recorded with digital hemispherical photographs every 20 m within the reaches and analyzed by the HemiView (Delta-T Devices) software package.

Task 2.3. Data Analysis

After 1 year, D/HF-disturbed sites had less riparian vegetation, more solar radiation, and significantly higher maximum and average temperatures as compared to control streams (Fig. 3). Burned streams with D/HF disturbance had less vegetation, more solar radiation, and higher maximum temperatures as compared to control streams. Burned streams without D/HF disturbance had similar vegetation, slightly more solar radiation, and slightly higher maximum temperatures as compared to control streams, but none of these differences were statistically significant. In comparing all of the 1 year old disturbances, it can be seen that while burned streams with D/HF disturbance receive by far the greatest solar radiation, the debris flow sites without fire have similar maximum temperatures (Fig. 3a-c).

Objective 3. Characterize the evolution of debris/hyperconcentrated flow impacts through time

Besides the immediate extirpation of fish, D/HFs may also have longer-term impacts on riparian vegetation, stream temperature, and other physical characteristics of streams in the time between disturbance and recovery. These long-term impacts to the stream may influence the productivity and trophic interactions of the aquatic ecosystem, as well as have direct impacts to the habitat suitability for fish many years after the actual disturbance. To look at the long-term impacts of D/HFs, roughly 10 and 40 year old disturbances will be examined and compared to both recently disturbed sites and to undisturbed control streams.

Task 3.1. Site Selection

Clusters of 1964 and 1995 disturbed sites and controls were chosen to look at the impacts of disturbance on stream heating and temperature after 40 and 10 years, respectively. We looked at 3 unburned streams disturbed by D/HFs in 1964, and 3 controls near the confluence of the middle and north forks of the Boise River (blue and purple labels, respectively, in the lower left corner of Fig. 2). We also looked at 3 burned streams with D/HF disturbances that occurred in 1995/1997, 3 streams that were burned and undisturbed by D/HFs, and 3 control streams (red, green, and purple labels, respectively, in the center of Fig. 2). Sites were chosen to have similar drainage areas, and to be located close to one another.

Task 3.2. Collect Field Data

Field methods are the same as Task 2.2.

Task 3.3. Data Analysis

It was found that 40 years after D/HF disturbance without fire, there was no statistically significant difference in riparian vegetation density, solar radiation, or summer temperature (Figs. 4a-c). Burned basins had an increase in maximum temperature, which was not statistically significant 10 years after the fire (Fig. 5c). Burned basins with D/HF disturbances that were 7

years old continued to show elevated maximum and average temperatures, as well as less riparian vegetation and greater insolation compared to control streams (Fig. 5a-c).

Disturbance and Recovery Trajectories

Combining these long-term results with the short-term results from Objective 2, provides insight regarding the response trajectories of stream temperature following different types of disturbance (Fig. 6). It can be seen that streams fully recover from D/HF disturbance in less than 40 years, though the exact timing and trajectory of recovery is uncertain. For burned streams which experience D/HF disturbance, there is no recovery after 7 years. Streams that are burned only show partial recovery after 10 years. The time to full recovery for these latter two cases is unknown.

The predicted patterns of disturbance by fire and D/HF, and its impact on hillside trees and streamside shrubs (Fig. 1), is borne out by an examination of radiation and shrub density data (Fig. 7). Results show decreasing solar radiation with increasing riparian shrub density for all 32 streams studied. The different disturbance classes plot into separate areas due to the interaction of the different disturbances with the hillside trees and riparian shrubs (Fig. 1). Undisturbed, control streams have a wide range of riparian shrub densities all with low solar radiation values (Fig. 7, green diamonds). Burned only streams have very similar riparian shrub densities but slightly elevated radiation values due to the removal of hillside trees by fire (Fig. 7, yellow triangles). D/HF disturbance removes riparian vegetation leading to elevated solar radiation inputs after one year as seen in the three points on the left of the figure (blue squares), but both vegetation and radiation values return to control levels after 40 years as seen in the three points in the center of the figure (blue squares). Fire- and D/HF-disturbed streams have lost both near-stream and hillside vegetation, giving them high radiation values (black circles). The observed relationship between vegetation and solar radiation, along with existing data on the rate of recovery of trees and shrubs, allows prediction of the full temporal trajectory of temperature recovery.

Objective 4. Create an assessment tool to identify channels impacted by debris/hyperconcentrated flows and to estimate the date of disturbance

This portion of the project was abandoned due to complexities beyond the intended scope of work, and because a more thorough, longer-term study did not suit the RMRS' needs at this time. See Report 1 (Jorde et al. 2004) for further detail.

Objective 5. Identify the topographic signature of bulking debris-flow initiation zones

Many of the D/HFs observed in the study area over the last three field seasons were the result of overland flow generated by intense thunderstorms on dry or burned hillsides, also known as "bulking" debris flows (Cannon et al. 1998; 2001). This "bulking" initiation is distinct from that of pore-pressure induced land sliding, where colluvial material liquefies once it begins to move (e.g., Benda and Dunne 1997; Montgomery and Dietrich 1994). This portion of the research seeks to explain the initiation of these "bulking" D/HFs in hillside channels and their topographic signature from the stream to the ridgeline.

The shape of a landscape reflects the dominant process that transports sediment across that landscape, and channel heads are a transition point between diffusive hillslope transport processes and advective channel processes (Smith and Bretherton 1972) (Fig. 8a). The

longitudinal profile from the ridge top down can be divided into a diffusive hillslope with a convex profile, a fluvial zone with a concave profile, and a transitional zone of varying curvature that connects the convex and concave curves. This zone can be looked at in profile or in slope-area diagrams (Fig. 8). The length of the transition zone will reflect the variability of the channel head-forming processes at a site.

The location of the channel head is not fixed because the rates of infiltration excess overland flow are not fixed, due to temporal variability in both precipitation and infiltration rates. This allows us to look at the location of the channel head in a probabilistic way, with a central tendency and a range of possible locations which become less likely farther from this "typical location" (e.g., Istanbullouglu et al. 2002).

A simple overland flow model run over surveyed topography can predict the point at which the critical shear stress is exceeded and the channel head formed for any particular rainfall intensity and duration. If a probability distribution of storms is used in this model, a probability distribution of channel head locations will be developed. This in turn can be used to model the relative dominance of fluvial and diffusive processes throughout the transition zone. If the sediment transport in the transition zone is defined as the sum of the sediment transport from each component process, then the slope in the transition zone can be modeled as a linear blending of the slopes of the two individual processes (Fig. 8b) (Tarboton et al. 1992). This complete model allows for examinations of the impact that topography has on sediment transport processes, as well as the reciprocal impact of sediment transport on topography.

Task 5.1. Site Selection

Ten hillsides that experienced recent gullying and D/HF initiation during the summers of 2003 or 2004 were chosen so that gullies and channel heads were easily identifiable. Sites with few trees and obstructions to the radio signal were chosen so that the differential GPS (DGPS) equipment could be used with real-time corrections. All sites were located in the same study area as streams surveyed for Objectives 2 and 3 (Fig 2).

Task 5.2. Collect Field Data

The longitudinal profile of the hillside was surveyed with one DGPS rover from the gully bottom to the ridgeline, with an average spacing of 1 m between points, and a three dimensional accuracy of at least 3 cm. The drainage area was surveyed with a second DGPS rover.

Task 5.3. Data Analysis

A one-dimensional model of the hillside channel profile will be created to see if stochastic rainfall events and sediment transport functions calibrated to literature values and field measurements can explain the measured profiles. This can be used to calculate the relative dominance of sediment transport processes at any point of the hillside profile, from 100% diffusive at the ridgeline, through a mixed transition zone, and to the 100% fluvial channel below.

Additional work on bulking debris-flow initiation

Additional work on the mechanisms of bulking debris-flow initiation was carried out during 2005 in support of Objective 5. Specifically, the proposed role of stepped channel profiles was examined as the causative factor in initiation (Cannon et. al. 2003). An additional

hillside survey indicated that hillsides and channels with stepped profiles erode soil less efficiently on a unit area basis (Fig. 9). This indicates that steps may actually inhibit the erosion of sediment as compared to planar channel bottoms, and make the generation of bulking debris flows less likely. We have proposed an alternative initiation mechanism based on altered fluid properties due to the addition of fine sediment. A literature review showed that increased amounts fine sediment in flowing water increases the capacity of the fluid to suspend additional fine material by altering the density and yield strength of the fluid. Hence, there is a positive feedback, where fine sediment in suspension leads to a greater capacity to further suspend sediment. The increased fluid density resulting from high suspended sediment concentrations has also been shown to increase the bedload transport capacity of the fluid (Rickenmann 1990). Together, the increased suspended and bedload transport capacities can explain the incorporation of sediment up to and beyond the sediment concentrations characteristic of debris flows. This work was presented in an invited talk at the 2005 Geological Society of America Meeting and is being prepared for publication (Welcker et. al. 2005b).

REFERENCES

Benda, L., and T. Dunne. 1997. Stochastic forcing of sediment supply to channel networks from landsliding and debris flow. Water Resources Research **33**:2849-2863.

Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: Fisheries and forestry interactions. *in* E. O. Salo and T. W. Cundy, editors. Streamside Management: Forestry and Fishery Interactions Conference. University of Washington, Institute of Forest Resources, Seattle, WA. pp. 191-232.

Cannon, S. H., C. Parrett, and M. Parise. 2003. Wildfire-related debris-flow generation through episodic progressive sediment bulking processes, western USA. Pages 1300 *in* D. Rickenmann and C. Chen, editors. Third International Conference: Debris-Flow Hazards Mitigation. Millpress, Rotterdam, Davos, Switzerland.

Cannon, S. H., E. R. Bigio, and E. Mine. 2001. A process for fire-related debris flow initiation, Cerro Grande fire, New Mexico. Hydrological Processes **15**:3011-3023.

Cannon, S. H., P. S. Powers, and W. Z. Savage. 1998. Fire-related hyperconcentrated and debris flows on Storm King Mountain, Glenwood Springs, Colorado, USA. Environmental Geology **35**:210-218.

Dunham, J. B., B. E. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management **23**:894-904.

Dwire, K. A., and J. B. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western USA. Forest Ecology and Management **178**:61-74.

Istanbullouglu, E., D. G. Tarboton, R. T. Pack, and C. H. Luce. 2002. A probabilistic approach to channel initiation. Water Resources Research **38**:14.

Istanbullouglu, E., D. G. Tarboton, R. T. Pack, and C. H. Luce. 2004. Modeling of the interactions between forest vegetation, disturbance and sediment yields. Journal of Geophysical Research.

Jorde, K., A. E. Rosenberger, N. E. Scheidt, C. W. Welcker, B. E. Rieman, C. H. Luce, J. B. Dunham, J. M. Buffington, J. A. McKean. 2004. Stream ecosystem response to wildfire. Ecohydraulics Research Group, University of Idaho, and USDA Forest Service, Rocky Mountain Research Station. Report 1 (unpub.), January 1, 2003 – December 31, 2003, Agreement Number 02-JV-11222014-196. 23 pp.

Jorde, K., A. E. Rosenberger, N. E. Scheidt, C. W. Welcker, B. E. Rieman, C. H. Luce, J. B. Dunham, J. M. Buffington, J. A. McKean. 2005. Stream ecosystem response to wildfire. Ecohydraulics Research Group, University of Idaho, and USDA Forest Service, Rocky Mountain Research Station. Report 2 (unpub.), January 1, 2004 – December 31, 2004, Agreement Number 02-JV-11222014-196. 46 pp.

Megahan, W. F. 1972. Subsurface flow interception by a logging road in mountains of central Idaho. Pages 350-356 *in* National Symposium on Watersheds in Transition, Fort Collins, CO. American Water Resources Association, Herndon, VA.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association **35**:397-409.

Montgomery, D. R., and W. E. Dietrich. 1994. Landscape dissection and drainage area-slope thresholds. *in* M. J. Kirkby, editor. Process Models and Theoretical Geomorphology. John Wiley & Sons, New York. pp. 221-246.

Noste, N. V., and C. L. Bushey. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. General Technical Report INT-239 Intermountain Research Station, USDA Forest Service, Ogden, UT. 21 pp.

Rickenmann, D. 1990. Bedload transport capacity of slurry flows at steep slopes. PhD. ETH Zurich, Zurich, Switzerland.

Smith, T., and F. Bretherton. 1972. Stability and the conservation of mass in drainage basin evolution. Water Resources Research **8**:1506-1529.

Tarboton, D. G., R. Bras, and I. Rodriguez-Iturbe. 1992. A physical basis for drainage density. Geomorphology **5**:59-76.

Welcker, C., J. M. Buffington, C. H. Luce, B. E. Rieman, and J. McKean. 2004. Impacts of mass wasting on channel morphology and stream temperature in mountain rivers of central Idaho. Eos Transactions. AGU, **85**(47), Fall Meeting Supplement, Abstract H53C-1271.

Welcker, C., J. M. Buffington, C. H. Luce, B. E. Rieman, and J. McKean. 2005a. Long-term impacts of fire and mass wasting on solar loading and stream heating in mountain streams of Central Idaho. Eos Transactions. AGU, **86**(52), Fall Meeting Supplement, Abstract H13K-5919.

Welcker, C., J. M. Buffington, C. H. Luce, B. E. Rieman, and J. McKean. 2005b. The potential influence of stair-step morphology on the initiation of bulking debris flows in southwestern Idaho, USA. Geological Society of America Abstracts with Programs, **37**(7), 35.

Whiting, P. J., and J. B. Bradley. 1993. A process-based classification system for headwater streams. Earth Surface Processes and Landforms **18**:603-612.

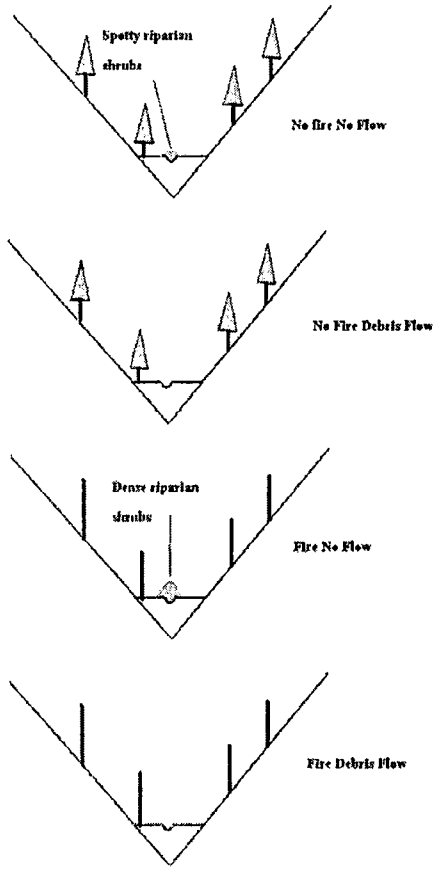


Figure 1. Four vegetation disturbance classes from all four different combinations of fire and D/HFs disturbance.

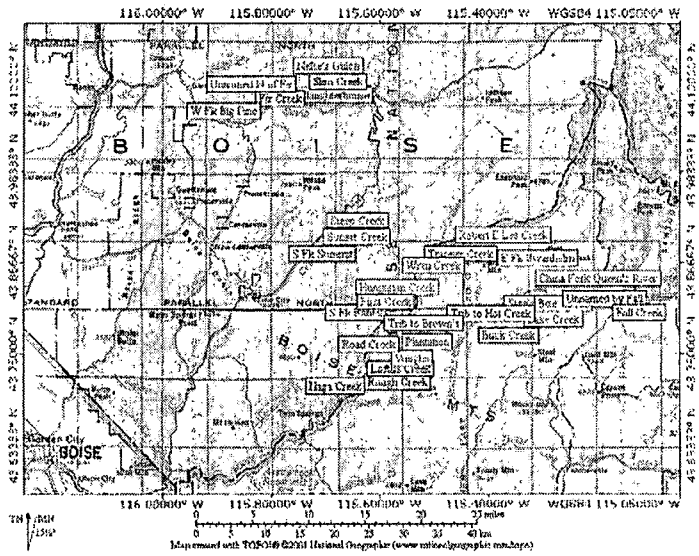


Figure 2. Streams surveyed during summer 2004. Purple text denotes control streams, blue text is used for unburned 1964 and 2003 D/HF-disturbed streams. Red text is used for burned 2004 and 1995/7 D/HF-disturbed streams. Green and black text shows undisturbed streams which were burned in 1995/7 and 2003, respectively.

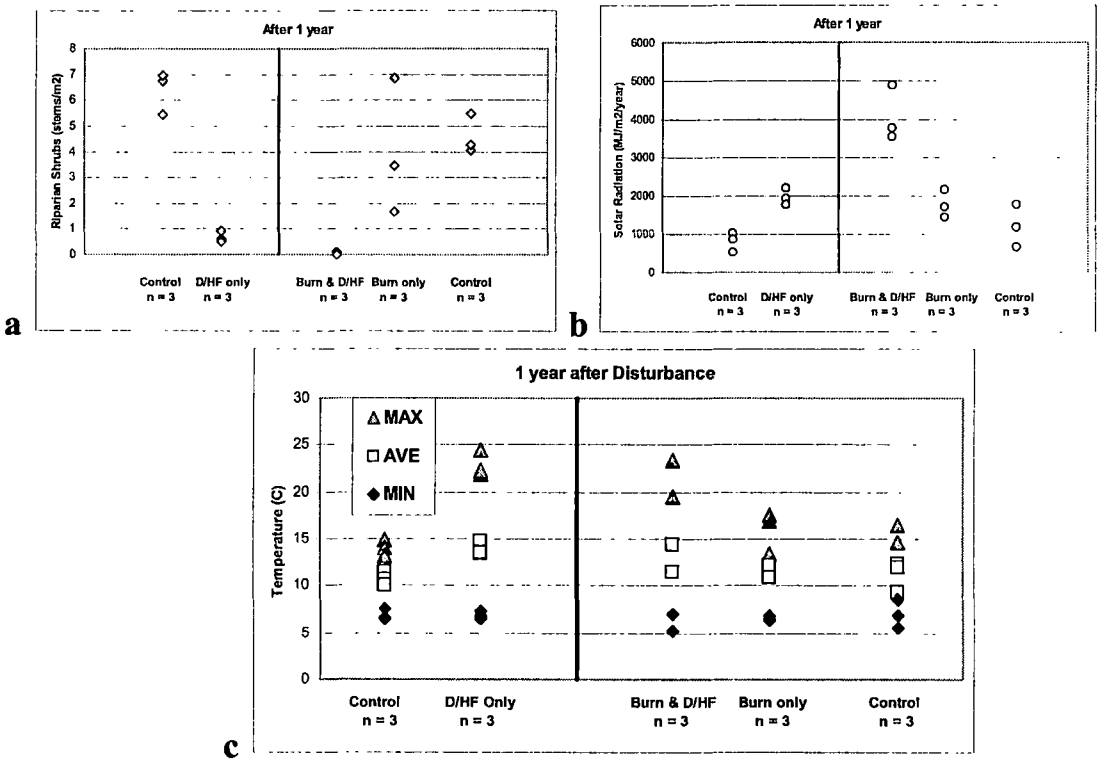


Figure 3. Results for 1 year old channel disturbances and control streams for a) riparian vegetation density, b) solar radiation, and c) summer-long maximum, average and minimum stream temperatures. Streams which experienced D/HF disturbance and fire, had significantly less vegetation, more radiation and increased maximum and average stream temperatures as compared to controls. Streams which experienced D/HF disturbance with no fire, had significantly less vegetation, more radiation and increased maximum stream temperatures as compared to controls. Streams which only experienced fire had similar vegetation, slightly higher radiation, and slightly higher maximum temperatures than controls, but none of these differences were significant. It should be noted that while fire and D/HF-disturbed streams have by far the most radiation, they have maximum temperatures similar to unburned, D/HF-disturbed streams.

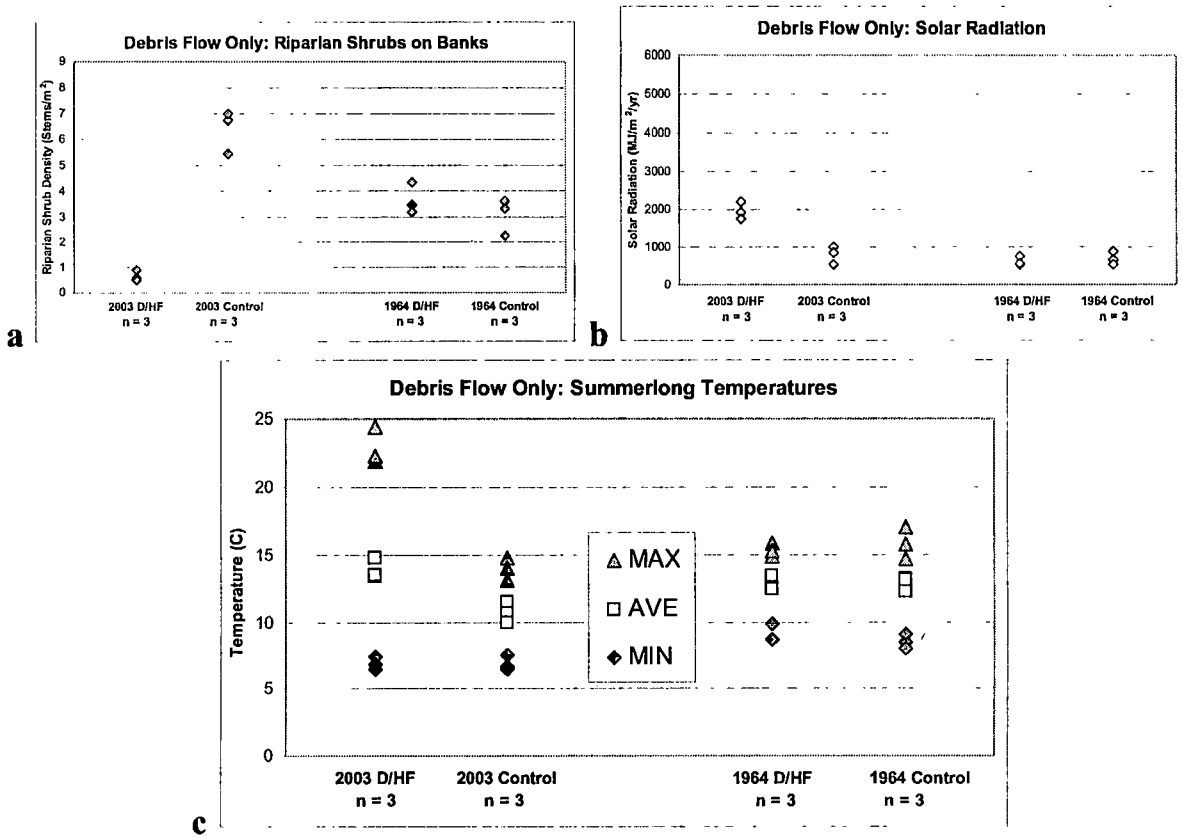


Figure 4. Results for 1 and 40 year old D/HF disturbances and control streams for a) riparian vegetation density, b) solar radiation, and c) summer-long maximum, average and minimum stream temperatures. While 1 year after disturbance, streams had significantly less vegetation, more radiation and increased maximum stream temperatures as compared to controls, there were no significant differences 40 years after disturbance. This implies that channels have fully recovered to pre-disturbance conditions after 40 years.

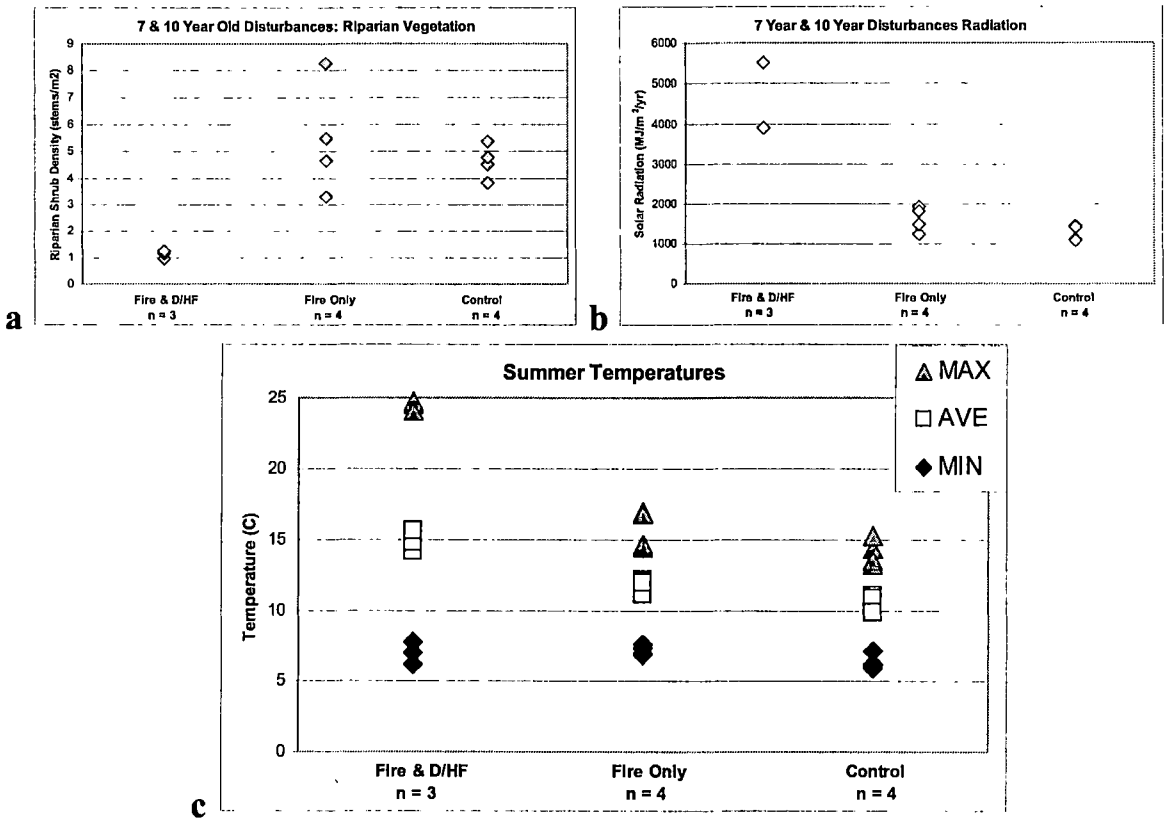


Figure 5. Results for a) riparian vegetation density, b) solar radiation, and c) summer-long maximum, average and minimum stream temperatures with 7 year old D/HF disturbance and 10 year old fire. Streams which experienced D/HF disturbance with fire, had significantly less vegetation, more radiation and increased average and maximum stream temperatures as compared to controls. Streams which only experienced fire had similar vegetation, slightly higher radiation, and slightly higher maximum temperatures than controls, but none of these differences were significant. For both the burned only and burned with D/HF disturbance categories, there is no recovery as compared to the 1 year old disturbances shown in Fig. 3.

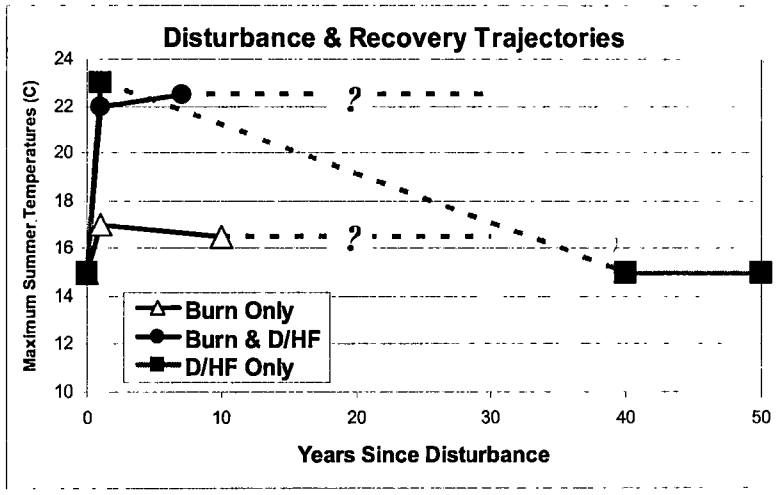


Figure 6. Partial disturbance and recovery trajectories for maximum summer temperatures after fire, fire and D/HF, and D/HF only. Each point in the graph represents the average for streams with a given disturbance type and time since disturbance shown in Figures 3-5. Control streams were used to represent pre-disturbance conditions (Year 0 in the figure). Portions of the trajectories with large uncertainties are shown as dotted lines. The D/HF Only trajectory shows increased water temperatures after one year with a return to pre-disturbance temperature by 40 years, but the shape of the intervening trajectory is unclear. Burn Only and Burn & D/HF show elevated temperatures 1 year after disturbance which have not declined 10 or 7 years after disturbance, respectively. The ultimate time to recovery in these streams is unknown.

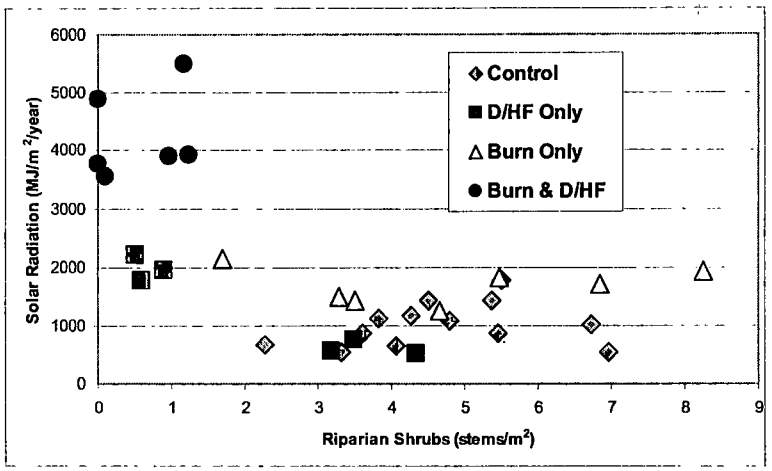


Figure 7. Decreasing solar radiation with increasing riparian shrub density for all 32 streams studied. The different disturbance classes plot into separate areas due to the interaction of the different disturbances with the hillside trees and riparian shrubs (Fig. 1). Undisturbed, control streams have a wide range of riparian shrub densities all with low solar radiation values (Fig. 7, green diamonds). Burned only streams have very similar riparian shrub densities but slightly elevated radiation values due to the removal of hillside trees by fire (Fig. 7, yellow triangles). D/HF disturbance removes riparian vegetation leading to elevated solar radiation inputs after one year as seen in the three points on the left of the figure (blue squares), but both vegetation and radiation values return to control levels after 40 years as seen in the three points in the center of the figure (blue squares). Fire- and D/HF-disturbed streams have lost both near-stream and hillside vegetation, giving them high radiation values (black circles).

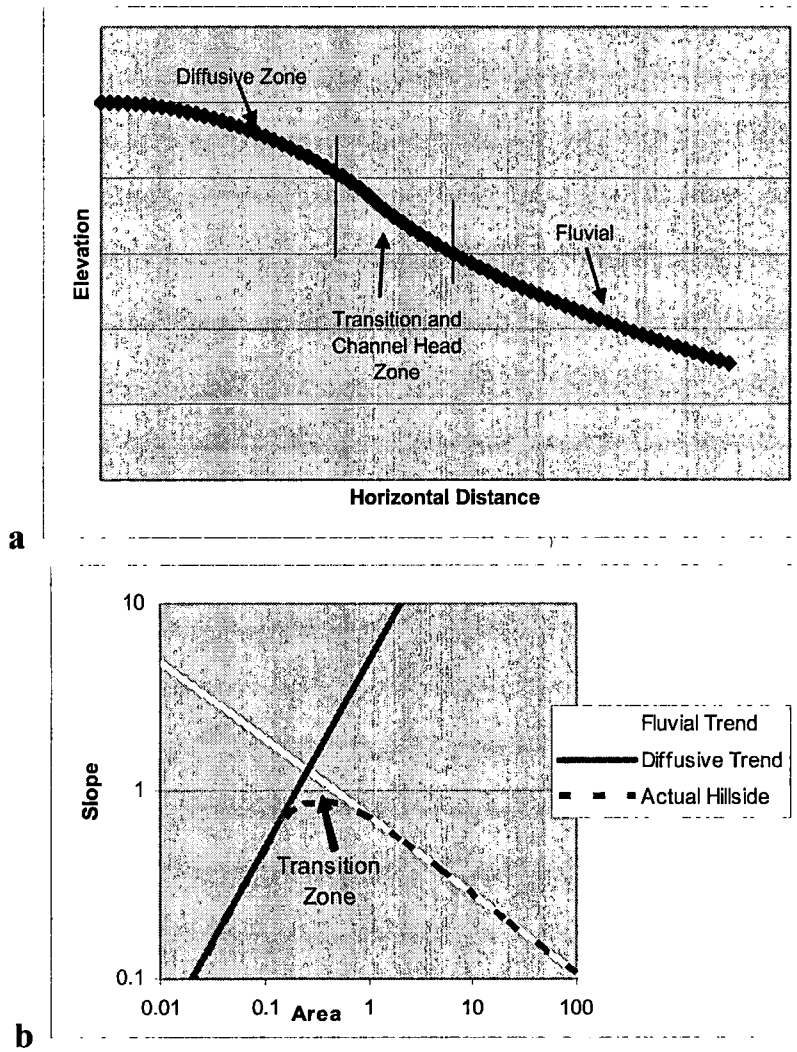


Figure 8. The transitional zone between fluvial and diffusive processes a) in profile and b) in an area–slope plot. In both graphs, the slope of the transitional zone is a combination of the slopes expected for solely fluvial or diffusive incision.

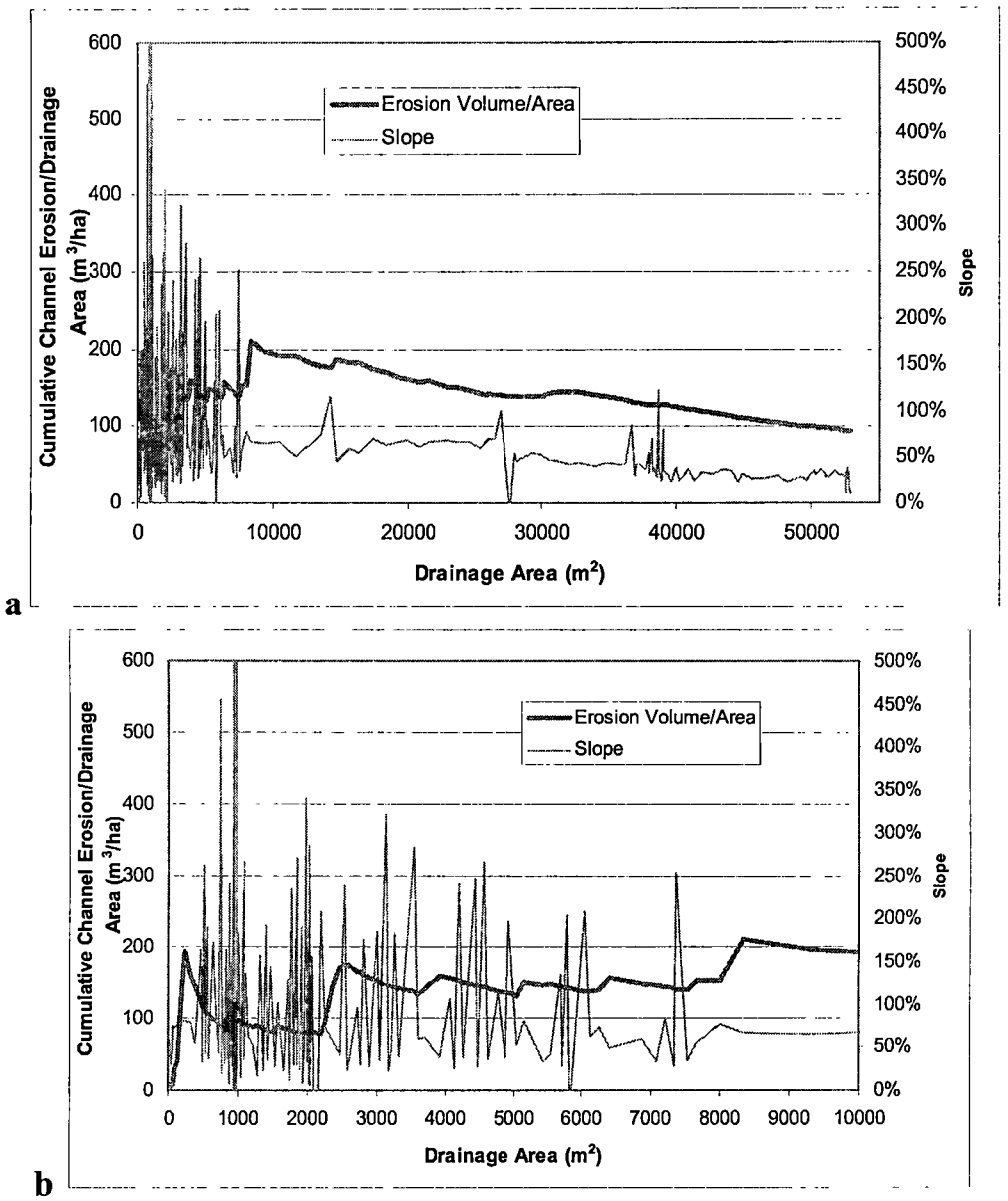


Figure 9. Hillside slope and erosion efficiency (volume of sediment eroded for a given drainage area) as a function of drainage area for a) the entire hillside from ridgeline (left) to base of the hill (right) and b) the upper portion of this hillside that initiated a bulking debris flow in summer 2005. The highly variable areas of the green slope line indicate where a stepped longitudinal profile is present. It can be seen that erosion efficiency tends to decline in areas with more steps. The orange line in both graphs is the first point down from the ridgeline where depositional evidence of debris flow rheology was seen.

RESEARCH AREA 2: STREAM SUCCESSION: CHANNEL CHANGES AFTER WILDFIRE DISTURBANCE

Masters Research of
Nicholas E. Scheidt

ABSTRACT

One concept in geomorphology is that vegetation is a fundamental control on sediment and water supplies to streams and, therefore, on downstream fluvial processes and channel morphology. Within this paradigm, wildfire has been implicated as a major driving force behind landscape erosion and changes to stream channels, periodically yielding pulses of sediment from uplands that may drive changes to stream channels. However, channel response to wildfire has not been well studied over long periods (>10 years), and the occurrence and nature of long-term changes in channel characteristics remain to be documented. The long-term effects of wildfire disturbance on channel characteristics were examined in moderate-gradient (2-4% slope), unconfined, mountain streams in the Idaho batholith. The study was designed using a space-for-time substitution, and three different times since wildfire were considered: recent (15-20 yrs.), mid (80-110 yrs.), and old (>150 yrs.). Characteristics of interest included measures of channel morphology (e.g., channel geometry, pool spacing, residual depth, substrate size) and wood (e.g., amount, location, function, size). Multi-response permutation procedures were used to measure between treatment variability. Results show that none of the 17 morphologic characteristics varied between treatments, and only 3 out of 25 wood characteristics varied between treatments ($\alpha = 0.10$). The lack of morphologic variability between treatments implies that wildfire disturbance does not have a long-term effect on channels of this stream type, suggesting that moderate-gradient, unconfined channels may act as relatively stable, potentially productive, refugia for aquatic organisms in areas prone to wildfire.

INTRODUCTION

The primary question of this thesis is "How do stream channels change after fire?" In forest communities, fire disturbance initiates vegetative succession (temporal changes in species composition, age distribution, and ecosystem function), with responses lasting decades to hundreds of years (Agee, 1993). There are no analogous data for stream channels following wildfires, yet there is a common belief among watershed professionals that stream channels are impacted by wildfire and subsequently follow a post-fire trajectory of recovery. This process is herein referred to as "channel succession", and is defined as a change in channel characteristics and stream habitat quality that coincides with terrestrial vegetative succession after fire disturbance. Limited data from the Oregon Coast Range suggest that streams attain optimal habitat condition at a mid-seral stage, on the order of 80-120 years after fire disturbance (Reeves et al., 1995). However, the generality of this response trajectory across different channel types and locations within a stream network is uncertain. For example, due to differences in process domains and susceptibility of channels to disturbance, we may expect fire-related response in high-gradient, confined streams that are dominated by debris flows to differ from that of low- or moderate-gradient, unconfined streams that are fluvially dominated (Montgomery and Buffington, 1998; Montgomery, 1999). There is a need to better understand channel succession across various stream types and regional settings. A comprehensive understanding of channel succession would help resource managers make better forest, fisheries, and fire management decisions related to stream channel condition. Here, channel response to wildfire is examined in moderate-gradient, high-elevation channels that are both prone to wildfire and provide important salmonid habitat in mountain basins.

Despite the common perception that post-fire channel succession occurs, the nature of the response trajectory and the relative roles of different physical drivers are largely unknown. Forest fires can cause short-term alteration of sediment supplies (Miller et al., 2003; Wondzell and King, 2003), the timing and size of peak flows (Moody and Martin, 2001) and spatial and temporal rates of wood recruitment (Benda et al., 2003). Alteration of these channel-forming processes may have a significant effect on channel morphology (Wolman and Miller, 1960; Wolman and Gerson, 1978; Harmon et al., 1986). Geomorphic significance of such alterations depends on 1) fire extent and severity; 2) physical setting (topography, geology, location within the stream network, and stream type); and 3) the frequency, magnitude, style, and timing of post-fire precipitation events (Swanson, 1981; Meyer et al., 1992; Meyer et al., 1995; Benda et al., 1998). Minshall et al. (1989) suggested that post-fire effects could be segregated into immediate, mid-term, and long-term categories. Immediate effects may include increases in stream temperature or potentially toxic substances (e.g., ammonia), or decreases in pH. Mid-term effects can be dramatic and typically peak within the first decade after fire; they are usually associated with fire-related changes in erosion and hydrologic regimes. Some previous research suggests that substantial channel recovery after floods can occur within a decade (Wolman and Gerson, 1978). Long-term effects are less dramatic and, potentially, coincide with in-stream wood dynamics associated with post-fire forest succession.

Several hypothetical response trajectories can be envisioned for how aquatic habitat quality might change over time due to wildfire disturbance. One hypothesis is that habitat quality is initially degraded, but slowly recovers over time (Figure 1, line A) (Minshall et al., 1989; Beechie et al., 2000). Here, the initial decrease in habitat quality is due to increased erosion and flooding, and the eventual increase in habitat quality is associated with increased abundance of

in-stream wood due to forest maturation. Whether this occurs over a few years or a few hundred years is not clear. Some have suggested that response times are relatively long (Reeves et al., 1995; Benda and Dunne, 1997a,b; Minshall et al., 1989), while other research suggests that physical habitat could adjust to changes in hydrology within a few years (Wolman and Gerson, 1978). A more complex hypothesis is that habitat degrades temporarily from a long-term marginal condition, then achieves a state better than the initial condition for some period, followed by a gradual decline to the long-term (Figure 1, line B). This idea is prevalent where gravel availability is limiting (Reeves et al., 1995). In these sediment-starved channels, sufficient time is needed for post-fire sediment pulses to replenish alluvial substrate, and for forest regrowth and the incorporation of newly recruited wood into this sediment to cause a maximum in channel complexity (i.e., habitat quality). A third hypothesis is that there is no strong change in habitat quality with time (Figure 1, line C), which might be seen in low- to moderate-gradient, unconfined streams. Such streams are typically buffered from direct impacts of post-fire debris flows, decreasing the probability of a large disturbance. Furthermore, storage of wood and coarse sediment within the floodplain of these channels may mitigate post-fire effects of altered basin hydrology or altered supply of riparian wood that would otherwise lead to stronger channel response. As a stream incises or migrates laterally due to post-fire changes in basin hydrology and increased peak flows, or due to decreased supply of wood recruited from burned riparian zones, it may encounter buried wood or coarse sediment that mitigates further incision and lateral migration, helping to stabilize the channel.

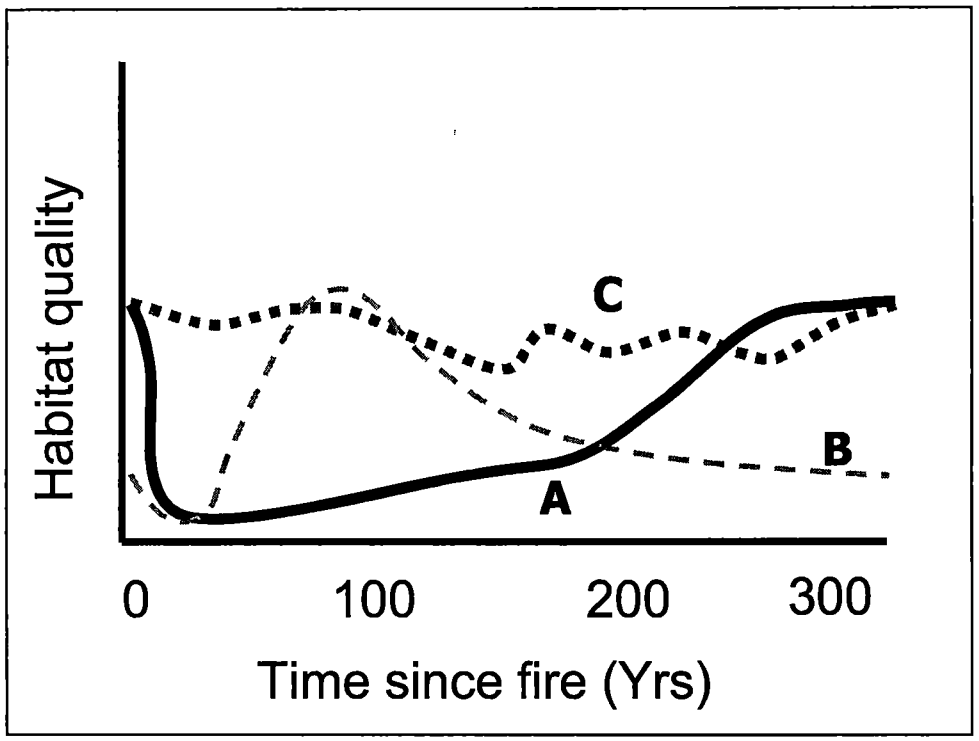


Figure 1. Hypothetical habitat quality response trajectories to wildfire.

This study investigates channel responses in moderate-gradient, unconfined, high-elevation basins that have experienced spatially extensive stand-replacing fires. The underlying hypothesis addressed is the idea that streams change systematically over time following wildfire disturbance. The focus on moderate-gradient, unconfined, high elevation streams is based on their importance for thermally sensitive salmonids. In these streams, direct impacts from debris flows and hyperconcentrated flows are excluded, and the focus is placed on post-fire changes in basin hydrology, upstream sediment supply (potentially influenced by debris flows and hyperconcentrated flows), and proximal riparian characteristics (supply of wood and bank strength from roots). Biologically, knowledge of recovery time scales is necessary to determine how likely simultaneous disturbance of several local populations might be, a key factor in local extinctions (Miller et al., 2003, Dunham et al., 2003, Rieman et al., 2003, Bisson et al., 2003).

STUDY DESIGN

A space-for-time substitution approach was used to examine the effects of wildfire on channel and wood characteristics (e.g., Welch, 1970). The analysis consisted of 3 treatments of time since fire: 15-20 years (recent), 80-110 years (mid), and >150 years (old). Several potentially confounding variables were identified, including geology, valley slope, valley confinement, elevation (which controls precipitation and vegetation), drainage area (a surrogate for discharge), glacial history, land use, and extent of burn. To control for these confounding variables, sites were selected that met the following criteria: 1) elevation between 1500-2000 meters; 2) watershed primarily located within the Idaho batholith (granite); 3) valley width greater than 4 bank-full channel widths; 4) valley slopes between 2.0-4.0%; 5) drainage area between 500-1200 hectares; 6) > 50% of the basin experienced a stand replacing wildfire, including the riparian stand; and 7) minimal anthropogenic disturbance (streams not affected by grazing, logging, and roads). Reaches were selected at relatively high elevations because wildfires in these locations are typically spatially extensive and stand replacing. The study reaches were limited to the Idaho batholith to control for geology. Valley width, valley slope and drainage area ranges were selected because the focus is on sites that are disconnected from hillslopes and direct sediment inputs from debris flows and hyperconcentrated flows. The percent of stand replacing burn was selected to insure that a significant portion of the basin burned. It was not possible to control for fire severity or post-fire precipitation events.

Candidate reaches were selected using 10 m digital elevation models (DEM) based on the first 5 control variables in combination with GIS coverages of fire history, land use, roads, and geology. Approximately 260 candidate streams were identified and further reduced to 45 sites

using aerial photographs (1:15,840) to evaluate the last two control variables. Each of these streams was field checked to validate characteristics estimated from the photos and DEM, and 30 streams were ultimately selected for sampling. After the field season, it was determined that bank-full discharge and valley slope were not sufficiently controlled at 7 of the 30 streams. This determination was made by graphically identifying outliers.

Unfortunately, it was not possible to directly control all of the potentially complicating variables in each case. It was especially difficult to find riparian stands of similar age to burned upland forests in the recent and mid treatments, suggesting longer fire return intervals for some riparian stands (e.g., Romme and Knight, 1981). Consequently, some study reaches in basins with recent and mid treatments have riparian stands older than the basin treatment. This complication allowed us to assess channel response to different combinations of altered hydrologic regime, sediment regime, and riparian stand characteristics by classifying the data according to three different burn definitions: time since basin burn, time since riparian burn, and time since synchronous burn (simultaneous basin and riparian burn) (Table 1). Appendices A1-3 show site characteristics stratified by burn classification.

A variety of channel, wood, and habitat characteristics were examined that might be responsive to post-fire changes in sediment supply, hydrology, and riparian conditions. Measured channel characteristics included grain size, bank-full channel geometry, slope, and residual pool depth. Measured wood characteristics included piece dimensions, embedment, orientation and location, function, spacing, and decay stage. Riparian stand characteristics (tree diameter, species, life stage, and burn class) were measured to help determine or confirm the fire history of each site.

Table 1. Burn classifications and sample sizes.

Basin burn

Treatment	Time since riparian burn (Years)	Time since basin burn (Years)	% basin burned	*n*
Recent	unspecified	15-20	>50	6
Mid	unspecified	80-110	>50	9
Old	unspecified	>150	>50	8
				total=23

Riparian burn

Treatment	Time since riparian burn (Years)	Time since basin burn (Years)	% riparian burned	*n*
Recent	15-20	unspecified	>50	4
Mid	80-110	unspecified	>40	7
Old	>150	unspecified	>47	12
				total=23

Synchronous burn

Treatment	Time since riparian & basin burn (Years)	% riparian burned	% basin burned	*n*
Recent	15-20	>47	>50	4
Mid	80-110	>40	>50	6
Old	>150	>47	>50	8
				total=18

STUDY SITES AND METHODS

Site characteristics

The study reaches were located at high elevations (1500-2000 m) in the Idaho batholith, which has a predominantly granitic geology (Figure 2). The average annual precipitation in the study area is between 1000 and 1500 millimeters and falls predominantly as snow at these elevations. Regional hydrology is snowmelt dominated, with peak flows typically occurring in late spring or early summer, although occasional intense summer thunderstorms can produce peak flows in small basins during the summer.

Native fish species potentially present in these streams include bull trout *(Salvelinus confluentus),* chinook salmon *(Onchorhynchus tshawytscha),* steelhead and rainbow trout (*O. mykiss),* and sculpin (*Cottus* spp.). Brook trout *(Salvelinus fontinalis)* is the most prevalent non-native species. The forest communities are dominated by subalpine fir (*Abies lasiocarpa*), white fir (*Abies concolor*), grand fir (*Abies grandis*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Forest types at the study sites were predominantly spruce–fir in the riparian zones and valley bottoms, with some inter-mixed lodgepole pine; lodgepole pine was more prevalent where severe fire occurred in the uplands. The predominant shrub found along the streams was mountain alder (*Alnus tenuifolia*). The historic (pre-European) fire regime is characterized by spatially extensive fires, typically stand replacing, with a return interval of 250 years (Morgan et al., 1996).

Study reaches were mainly third order streams (Horton, 1945), located away from major tributary junctions. Channel-reach morphologies were mostly pool-riffle and wood-forced pool-riffle, however one reach (Frank Brown Creek) had a plane-bed morphology (morphologic definitions of Montgomery and Buffington, 1997).

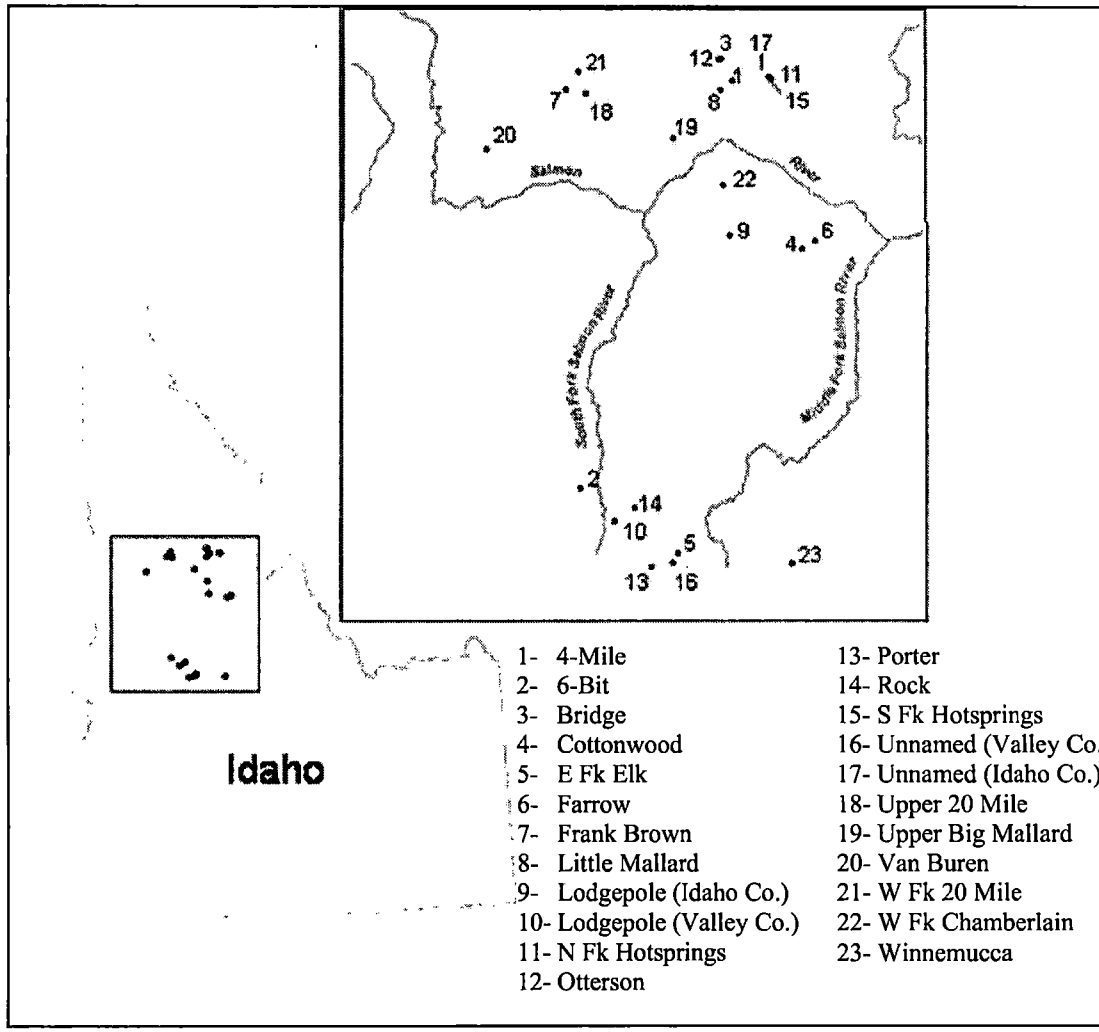


Figure 2. Location of study sites.

Channel morphology

A pilot study was conducted during the summer of 2002 to determine the sampling interval required to accurately represent reach-scale variation of channel width, depth, and surface grain size in mountain gravel-bed streams of central Idaho (C. H. Luce, unpublished data). No serial correlation was found beyond eight channel widths in that study; so each of our streams was characterized by 10 cross sections spaced 8 channel widths apart for a total reach length of 80 channel widths.

Cross sections, stream slope, and valley slope were measured with an engineer's level, measuring tape and stadia rod. Bank-full depth was measured relative to the bank-full elevation, defined as the point where stream flow spills onto the floodplain. In addition, the active channel depth was measured relative to the active channel elevation, defined by a convex break in the bank slope and a change to finer-grained sediments or, in the absence of those indicators, by the extent of riparian vegetation. The active channel depth was examined because it is affected by smaller, more frequent flows and, therefore, may be a more responsive indicator of fire-related disturbance than the bank-full depth.

The maximum residual depth was measured between each cross section, and was defined as the deepest point between two cross sections minus the associated downstream riffle-crest depth (a variant of Lisle's (1987) method for residual pool depths). Pools were inventoried, and the location of the center of each pool was recorded to determine exact spacing between pools. Pools were defined as topographic depressions either as long or as wide as the local active channel width. The residual depth of each pool was measured and the dominant sediment size was estimated within a 10 cm radius at the points of maximum pool depth and riffle-crest depth according to the substrate classes in Appendix A4. Wood was also used as a substrate class (organic substrate) at riffle crests, because it is resistant to erosion and often forms the riffle crest in these forest streams.

Sediment

A stratified random sampling technique was used to measure reach-average surface grain size. Two hundred grains were systematically sampled at equal intervals along the stream length (about every 0.4 channel widths). At each sample location, the bed width was divided into 9

evenly spaced sections and one section was randomly selected for sampling. A single grain was randomly obtained from the selected section using the Wolman (1954) pebble count technique and measured with a ruler to the nearest millimeter.

Riparian stand characteristics

Variable plot basal area cruises were conducted in the riparian zone of each reach using a 10 basal area factor prism (Dilworth and Bell, 1981). The plot dimensions in variable plot cruises depend on tree diameter, with greater diameter trees having larger plot areas. This technique ensures adequate sampling of all tree sizes, which is not ensured with small fixed area plots. Variable plot cruises enable small subsamples to accurately represent stand densities for various different diameter classes. Ten plots were established at cross-section intervals (8 channel widths) and measurements were conduced at the bank-full elevation; one half of the plot on each side of the stream. Data collected included diameter at breast height, tree species, life stage (Table 2), burn class (Table 3), and determination of whether the tree was dominant or subdominant with respect to the surrounding stand. Tree diameters were estimated, and one tree was randomly selected for true diameter measurement and coring. Paired observations of measured and estimated diameters were used to create a regression for predicting actual diameters of unmeasured trees.

Table 2. Tree age classification

	Alive*	Recently deceased	Young snag	Snag	Old snag
Needles	green	red/orange	none	none	none
Fine Branches	all	all	some	none	none
Bark	solid	solid	>50%	<50%	none
Wood	hard	hard	hard	mostly hard	mostly soft

*Life stage is assigned according to which particular column a tree most accurately fits.

Table 3. Burn categories

1	No evidence of burn
2	Scarred, but not dead
3	Dead, limbs/needles present
4	Dead, limbs not present

Wood

Several wood characteristics were analyzed that might be responsive to post-fire changes in sediment supply, hydrology, and riparian conditions. These included piece distribution, diameter, length, species, embedment, anchoring, orientation to flow, vertical location, function, cross-sectional extent, and decay/wearing class. Wood was classified as pieces longer than 1 m and greater than 10 cm in diameter (Swanson et al., 1976), and was measured over the entire reach length of 80 channel widths. The distance between the centers of each piece of wood was measured to determine the spatial distribution of wood within each study reach. Regressions between observed and estimated log diameters were developed, as was done for standing wood in the riparian zone. The length was measured to the nearest meter, and tree species was identified when possible. Embedment of each piece was classified as follows: bank embedded, bed embedded, both, or neither. Pieces were considered embedded if more than 50% of the bole diameter was buried. Anchoring was defined as still attached to the ground by roots in the place of growth. The orientation to flow was assigned as 0, 45, or 90 degrees to the centerline of the bank-full channel. The vertical position of each piece of wood was classified as either above or below the bank-full elevation. Each piece of wood was divided into quarters by length, and each quarter was assigned a function, multiple functions, or no function according to the following

categories: 1) no function–does not meet any of the following classes; 2) forming a pool; 3) associated with a pool–within a pool at or below bank-full stage, but not the dominant cause for pool scour; 4) deflecting flow into the bank; 5) armoring the bank from fluvial erosion; 6) armoring the bed–partially buried in the bed, with sediment surrounding it on both the upstream and downstream sides; and 7) damming sediment–physical barrier to downstream sediment movement, causing upstream aggradation.

The extent to which each piece of wood spanned the channel was measured as a percentage of the bank-full width (0-200%, measured in increments of 25%). A piece more than 100% across the channel was one that was over/in the channel more than once. For example, a piece that completely crossed the channel twice by spanning a river bend was classified as 200% across the channel. Decay/wearing classes were assigned to each piece of wood according to the categories shown in Appendix A5.

DATA ANALYSIS

Statistical tests

Multi-response permutation procedures (MRPP) were used to test between-treatment variability and conduct pair-wise comparisons ($\alpha = 0.10$) (Mielke et al., 1984). MRPP was selected because it is a nonparametric test that compares the distribution of data sets. MRPP can be thought of as a comparison between medians and interquartile ranges, and is similar to an analysis of variance. However, it does not actually compare medians and interquartile ranges, just the cumulative distance between observations. Calculations were done with an Excel macro created by Rudy King of the USDA Forest Service, Rocky Mountain Research Station Statistics

Unit (version, 4/2004). The exponent v in this macro is set equal to one, after recommendations of Mielke and Berry (1983) and Zimmerman et al. (1985). The Pearson type III approximation was used to reduce computation time (Mielke et al., 1981; Berry and Mielke, 1983; Iyer et al., 1983), which is an excellent approximation to exact MRPP analyses (Mielke and Berry, 1982; Mielke et al., 1982). Quantile-Quantile (*Q-Q*) plots were created for spatially distributed and length-scaled characteristics (wood lengths and distribution, pool depths and spacing, etc.). *Q-Q* plots graphically show whether two data sets have similar cumulative distributions relative to a one-to-one reference line, thereby providing a means to visualize differences between treatments. Here, constructed *Q-Q* plots aggregate all data from each treatment and treat each sample independently, ignoring pseudoreplication. For example, while approximately 300 pieces of wood may have been sampled in each stream, statisticians would not consider these independent samples because they come from the same stream.

Percent burn

The percentage of the stand burned in each treatment (recent, mid, or old fire) was evaluated both for the entire basin and for the riparian stand alone. The percent of the basin burned since 1910 was determined from aerial photographs. Burned areas were evaluated by tree crown size and stand density.

The percent of the riparian stand burned in the recent treatment was calculated with the burn categories (Table 3) by dividing the number of fire-killed trees by the number of living trees multiplied by 100. This technique is an underestimate of how many trees were actually fire-killed, because fire-toppling may have caused approximately 70% of the fire-killed trees to fall (visual observation).

Calculating the percent of the riparian stand burned in the mid and old treatments was more complex due to longer times since disturbance. Lodgepole pine and spruce were assessed as pioneer species, assuming that an age cohort of this species was indicative of forest response to fire. Age cohorts of pioneer species were graphically identified and used to help determine or confirm the time since fire. For example, at Frank Brown Creek the greatest number of trees was recruited in the period of 1913-1903 (Figure 3). This peak is predominantly composed of two cohorts, spruce and lodgepole pine. The age of these cohorts agrees with fire history data (provided by Pat Green, Nez Perce National Forest) and, therefore, it was concluded that these cohorts were recruited in response to wildfire. The fraction of the riparian stand that was burned was then determined by dividing the number of pioneer individuals by the total number of individuals. However, the values estimated from this approach were lower than those found with the recent riparian burn technique. Consequently, these techniques may not be directly comparable. The actual percentages of riparian trees burned in the mid and old treatments lie somewhere between the percent of pioneer species younger than the time since fire and the total number of species younger than the time since fire, as true fir can sometimes regenerate after fire (Anne Black, personal communication). This was the case for Otterson Creek, where 98% of the trees were fire regenerated, of which 78% were true fir. Appendix A7 shows the time of fire and percent of the riparian and basin stands burned for each study site.

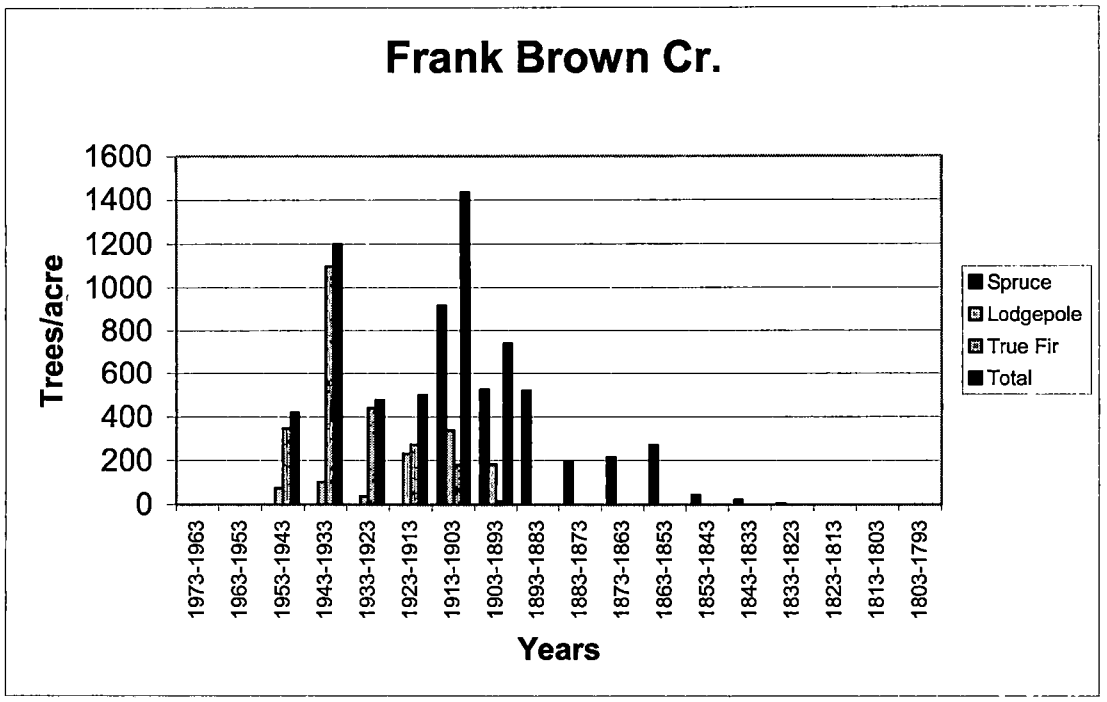


Figure 3. Tree density and age of recruitment by species.

Burn categories

Three burn classifications were used to isolate different potential drivers of post-fire change: time since basin burn; time since riparian burn; and time since synchronous basin and riparian burn. The basin burn category captures changes in channel morphology due to altered upstream hydrologic and sediment regimes for conditions where more than 50% of the contributing area experienced a stand-replacing burn. In contrast, the riparian burn category describes local changes in wood recruitment (size, amount, and frequency of wood input) that may, in turn, alter channel hydraulics and morphology (e.g., Montgomery et al., 1995; Buffington and Montgomery, 1999); the low rates of fluvial transport of wood into and out of these sites (due to relatively low channel slopes and narrow bank-full widths) ensures a focus on local wood recruitment for this burn category. Finally, the synchronous burn category evaluates the

combined effects of these factors (changes in upstream hydrologic and sediment regimes, and changes in local wood recruitment).

The MRPP analysis was conducted for each of the above burn classifications to systematically examine the different scales and types of disturbance that could influence channel characteristics. Only the riparian and synchronous burn classifications were used in the wood analysis in order to focus on the succession of wood characteristics and consequent channel impacts initiated by fire disturbance.

RESULTS

Overview

Results show that only 3 of 25 wood characteristics (Table 4) and 0 of 18 channel characteristics differ statistically across the study reaches (Table 5). All *P*-values presented herein are for MRPP results, unless otherwise specified. Appendix 6 reports site characteristics for each stream.

Table 4a. Results of MRRP tests on wood characteristics for data stratified by time since riparian burn.

Wood characteristics	Riparian Burn Recent[+]		Mid		Old		*P*
Pieces/100m	84.7	14.3	58.8	26.8	73.4	13.9	0.112
Functional pieces/100m	46.0	14.3	39.4	13.7	46.8	13.9	0.921
Non-functional pieces/100m	46.8	12.5	19.4	10.5	24.0	11.1	0.032*
Piece diameter (cm)	19.4	2.4	18.2	1.7	19.4	2.3	0.354
Variance in diameter	83.0	42.1	54.7	4.2	66.9	35.3	0.302
Length (m)	2.6	0.6	2.7	0.4	2.9	0.9	0.628
Variance in length	3.5	1.6	3.6	1.5	5.1	4.9	0.101
Piece spacing (m)	1.2	0.2	1.5	0.8	1.2	0.3	0.169
Functional piece spacing (m)	2.1	0.9	2.3	0.8	2.0	0.7	0.869
Volume/100m	43.5	11.4	26.9	12.4	34.3	25.1	0.104
Proportion of pools formed by LWD	0.3	0.1	0.4	0.1	0.3	0.4	0.554
0 degree orientation (pieces/total # of pieces)	24.2	5.0	27.9	7.0	27.6	8.0	0.380
45 degree orientation (pieces/total # of pieces)	45.8	4.0	38.8	13.0	41.2	9.0	0.238
90 degree orientation (pieces/total # of pieces)	29.4	4.0	33.3	13.0	32.5	10.0	0.715
Only above bankfull (pieces/100m)	16.3	10.3	4.0	2.0	6.5	3.1	0.006*
Only below bankfull (pieces/100m)	48.1	11.1	43.8	17.1	46.9	19.5	0.652
Above and below bankfull (pieces/100m)	21.3	13.4	18.3	9.6	16.2	12.5	0.372
Bank embedded (pieces/100m)	22.6	17.2	25.0	12.8	23.4	12.1	0.977
Bed embedded (pieces/100m)	8.9	9.6	10.7	9.0	9.3	12.1	0.962
Not embedded (pieces/100m)	55.2	19.3	25.9	6.4	36.6	17.0	0.063*
Pieces anchored/100m	7.8	3.4	9.0	3.1	5.9	3.1	0.320
0% across channel (pieces/total # of pieces)	1.0	3.0	2.0	4.0	4.0	6.0	0.234
25% across channel (pieces/total # of pieces)	52.0	30.0	51.0	15.0	55.0	23.0	0.901
50% across channel (pieces/total # of pieces)	15.0	5.0	13.0	2.0	15.0	2.0	0.777
75% across channel (pieces/total # of pieces)	9.0	4.0	9.0	3.0	7.0	5.0	0.900
100% across channel (pieces/total # of pieces)	17.0	17.0	20.0	11.0	18.0	14.0	0.833
Function: Forming a pool (Quarters/100m)	5.7	2.1	7.9	6.2	2.8	4.6	0.282
Function: Associated with a pool (Quarters/100m)	37.0	47.4	39.0	16.7	29.9	42.1	0.910
Function: Deflecting flow into bank (Quarters/100m)	1.5	0.7	1.3	2.5	1.7	3.1	0.579
Function: Armoring the bank (Quarters/100m)	57.7	16.3	38.7	15.8	43.9	9.8	0.467
Function: Armoring the bed (Quarters/100m)	13.6	10.7	16.1	17.9	17.5	16.6	0.576
Function: Damming sediment (Quarters/100m)	19.7	9.3	24.4	6.9	26.5	10.5	0.577

[+] Median values of stream means are on the left of each treatment column, and interquartile ranges on the right (underlined). Significant differences ($P<0.10$) are marked with an asterisk *.

Table 4b. Results of MRRP tests on wood characteristics for data stratified by time since synchronous riparian and basin burn.

Wood characteristics	Synchronous Burn Recent[+]		Mid		Old		*P*
Pieces/100m	84.7	14.3	64.3	24.8	77.4	10.2	0.190
Functional pieces/100m	46.0	14.3	43.2	16.2	51.1	12.3	0.748
Non-functional pieces/100m	46.8	12.5	21.1	8.7	24.0	7.3	0.042*
Piece diameter (cm)	19.4	2.4	18.3	1.3	19.3	2.3	0.607
Variance in diameter	83.0	42.1	54.9	3.2	59.5	26.2	0.314
Length (m)	2.6	0.6	2.8	0.4	2.9	0.8	0.819
Variance in length	3.5	1.6	3.9	1.2	5.1	4.5	0.103
Piece spacing (m)	1.2	0.2	1.5	0.6	1.2	0.2	0.310
Functional piece spacing (m)	2.1	0.9	2.1	0.8	1.8	0.5	0.822
Volume/100m	43.5	11.4	27.1	7.5	34.3	18.4	0.115
Proportion of pools formed by LWD	0.2	0.2	0.4	0.2	0.4	0.3	0.670
0 degree orientation (pieces/total # of pieces)	24.2	2.3	27.6	6.6	29.2	5.7	0.321
45 degree orientation (pieces/total # of pieces)	45.8	3.4	35.4	12.0	38.3	7.1	0.152
90 degree orientation (pieces/total # of pieces)	29.4	4.4	35.1	11.6	29.9	10.1	0.666
Only above bankfull (pieces/100m)	16.3	10.3	4.0	2.1	6.5	3.1	0.009*
Only below bankfull (pieces/100m)	48.1	11.1	45.0	10.5	55.0	12.9	0.468
Above and below bankfull (pieces/100m)	21.3	13.4	15.2	10.1	15.0	11.6	0.397
Bank embedded (pieces/100m)	22.6	17.2	19.8	13.2	24.9	10.1	0.869
Bed embedded (pieces/100m)	8.9	9.9	11.8	10.3	9.3	13.0	0.942
Not embedded (pieces/100m)	55.2	19.3	25.9	3.7	36.6	17.0	0.137
Pieces anchored/100m	7.8	3.4	9.0	0.7	5.9	2.2	0.370
0% across channel (pieces/total # of pieces)	1.3	2.7	3.2	3.3	5.0	6.6	0.128
25% across channel (pieces/total # of pieces)	51.1	31.0	48.0	13.9	56.6	16.6	0.773
50% across channel (pieces/total # of pieces)	14.7	5.4	12.5	2.3	15.2	1.9	0.760
75% across channel (pieces/total # of pieces)	8.6	3.8	8.7	1.6	6.6	1.9	0.545
100% across channel (pieces/total # of pieces)	16.8	15.9	23.2	12.2	13.0	12.8	0.626
Function: Forming a pool (Quarters/100m)	5.7	2.1	7.5	6.7	3.2	6.3	0.403
Function: Associated with a pool (Quarters/100m)	37.0	47.4	39.1	15.7	29.9	60.2	0.874
Function: Deflecting flow into bank (Quarters/100m)	1.5	0.7	1.6	2.8	1.7	2.6	0.639
Function: Armoring the bank (Quarters/100m)	57.7	16.3	34.7	10.9	43.4	6.3	0.109
Function: Armoring the bed (Quarters/100m)	13.6	10.7	19.7	20.5	17.5	9.1	0.608
Function: Damming sediment (Quarters/100m)	19.7	9.3	24.2	3.9	30.0	9.3	0.371

Median values of stream means are on the left of each treatment column, and interquartile ranges on the right (underlined). Significant differences ($P<0.10$) are marked with an asterisk *.

Table 5a. Results of MRRP tests on channel characteristics for data stratified by time since basin burn.

Channel characteristic	Basin Burn Recent[+]		Mid		Old		*P*
Max. residual depth between cross-sections (m)	0.29	0.08	0.27	0.10	0.29	0.08	0.909
Variance max. residual depth	0.007	0.003	0.011	0.005	0.011	0.006	0.597
Residual pool depth (m)	0.27	0.04	0.28	0.02	0.31	0.07	0.706
Var. in residual pool depth	0.01	0.003	0.01	0.015	0.01	0.008	0.803
Pool spacing (active channel widths)	4.91	2.69	3.71	1.30	5.71	4.18	0.702
$D_{50\ (mm)}$	29.75	47.13	17.00	21.50	28.25	19.50	0.741
Sinuosity (m/m)	1.26	0.13	1.21	0.26	1.23	0.08	0.889
Cross section area (m^2)	1.59	0.94	1.99	0.46	2.10	0.42	0.514
Hydraulic radius (m)	0.39	0.07	0.39	0.04	0.36	0.03	0.546
Channel width (m)	2.93	0.81	3.47	0.92	3.93	1.28	0.185
Var. channel width	0.40	0.593	0.65	0.689	0.97	0.521	0.311
Channel depth (m)	0.23	0.04	0.26	0.06	0.27	0.09	0.361
Var. channel depth	0.004	0.004	0.005	0.002	0.004	0.003	0.666
Bankfull depth (m)	0.42	0.14	0.43	0.02	0.40	0.05	0.335
Var. bankfull depth	0.006	0.006	0.007	0.003	0.005	0.002	0.507
Width-depth ratio[#] (m/m)	15.28	2.32	13.26	2.22	14.70	5.96	0.569

Median values of stream means are on the left of each treatment column, and interquartile ranges on the right (underlined). No characteristics are significantly different ($P<0.10$).

[#] Values for the active channel.

Table 5b. Results of MRRP tests on channel characteristics for data stratified by time since riparian burn.

Channel characteristic	Riparian Burn						
	Recent[+]		Mid		Old		*P*
Max. residual depth between cross-sections (m)	0.30	0.02	0.29	0.11	0.25	0.10	0.327
Variance max. residual depth	0.008	0.006	0.011	0.005	0.009	0.006	0.270
Residual pool depth (m)	0.28	0.03	0.28	0.05	0.30	0.09	0.841
Var. in residual pool depth	0.08	0.07	0.10	0.07	0.08	0.07	0.786
Pool spacing (active channel widths)	4.41	2.12	3.87	2.40	5.01	4.03	0.376
D_{50} (mm)	21.50	20.75	34.00	37.50	27.00	24.75	0.732
Sinuosity (m/m)	1.31	0.17	1.25	0.14	1.20	0.13	0.122
Cross section area (m^2)	1.98	1.05	1.69	0.36	2.10	0.56	0.635
Hydraulic radius (m)	0.42	0.07	0.39	0.03	0.36	0.03	0.121
Channel width (m)	3.22	1.04	3.12	0.47	3.89	1.14	0.799
Var. channel width	0.71	0.51	0.62	1.09	0.89	0.71	0.858
Channel depth (m)	0.24	0.02	0.24	0.05	0.26	0.11	0.515
Var. channel depth	0.005	0.002	0.004	0.003	0.004	0.002	0.929
Bankfull depth (m)	0.47	0.11	0.43	0.03	0.40	0.08	0.217
Var. bankfull depth	0.008	0.004	0.007	0.003	0.005	0.002	0.656
Width-depth ratio[#] (m/m)	14.02	2.78	13.12	4.22	14.83	3.10	0.878

Median values of stream means are on the left of each treatment column, and interquartile ranges on the right (underlined). No characteristics are significantly different ($P<0.10$).

[#] Values for the active channel.

Table 5c. Results of MRRP tests on channel characteristics for data stratified by time since synchronous burn.

Channel characteristic	Synchronous Burn Recent[+]		Mid		Old		*P*
Max. residual depth between cross-sections (m)	0.30	0.02	0.28	0.09	0.29	0.08	0.565
Variance max. residual depth	0.008	0.006	0.012	0.002	0.011	0.006	0.833
Residual pool depth (m)	0.28	0.03	0.29	0.06	0.31	0.07	0.904
Var. in residual pool depth	0.08	0.07	0.13	0.08	0.11	0.08	0.819
Pool spacing (active channel widths)	4.41	2.12	3.69	0.52	5.71	4.18	0.521
D_{50} (mm)	21.50	20.75	15.00	17.13	28.25	19.50	0.842
Sinuosity (m/m)	1.31	0.17	1.34	0.21	1.23	0.08	0.518
Cross section area (m^2)	1.98	1.05	2.02	0.43	2.10	0.42	0.677
Hydraulic radius (m)	0.42	0.07	0.41	0.04	0.36	0.03	0.266
Channel width (m)	3.22	1.04	3.50	0.83	3.93	1.28	0.569
Var. channel width	0.71	0.51	1.23	0.86	0.97	0.52	0.708
Channel depth (m)	0.24	0.02	0.26	0.05	0.27	0.09	0.484
Var. channel depth	0.005	0.002	0.005	0.002	0.004	0.003	0.956
Bankfull depth (m)	0.47	0.11	0.44	0.03	0.40	0.05	0.232
Var. bankfull depth	0.008	0.004	0.007	0.003	0.005	0.002	0.498
Width-depth ratio[#] (m/m)	14.02	2.78	14.02	3.09	14.70	5.96	0.752

Median values of stream means are on the left of each treatment column, and interquartile ranges on the right (underlined). No characteristics are significantly different ($P<0.10$).

[#] Values for the active channel.

Wood characteristics

Two wood characteristics varied in both the riparian and synchronous burn classifications: 1) the number of pieces only above bank-full and 2) the number of non-functional pieces. The riparian burn classification had one additional significant difference: the number of pieces not embedded in the bank or bed.

Comprehensive identification of wood species was not possible with the techniques employed, and therefore it was not possible to run a statistical analysis on wood species type. The sample size of pieces that crossed the channel more than once (>100%) was also too small for statistical analysis.

Location of wood within cross sections

The vertical position of wood within cross sections was classified as below bank-full, above, or both above and below. Wood classified as only above bank-full either bridged the bank-full channel or had greater than 1 m of length cantilevered above bank-full. Results show a significant difference in the amount of wood that is only above bank-full for both the riparian and synchronous burn classifications (P=0.006 and 0.009, Tables 4a-b, respectively). The results for the riparian burn classification are presented as an example (Figure 4), and are typical of the synchronous burn. The amount of wood above bank-full in the recent treatment is significantly greater than both mid and old treatments (P=0.006 and 0.040, respectively), while the amount of wood above bank-full in the old treatment is also significantly greater than the mid treatment (P=0.057). However, there is no significant difference across treatments in terms of the number of pieces below bank-full or both above and below bank-full (Figure 4).

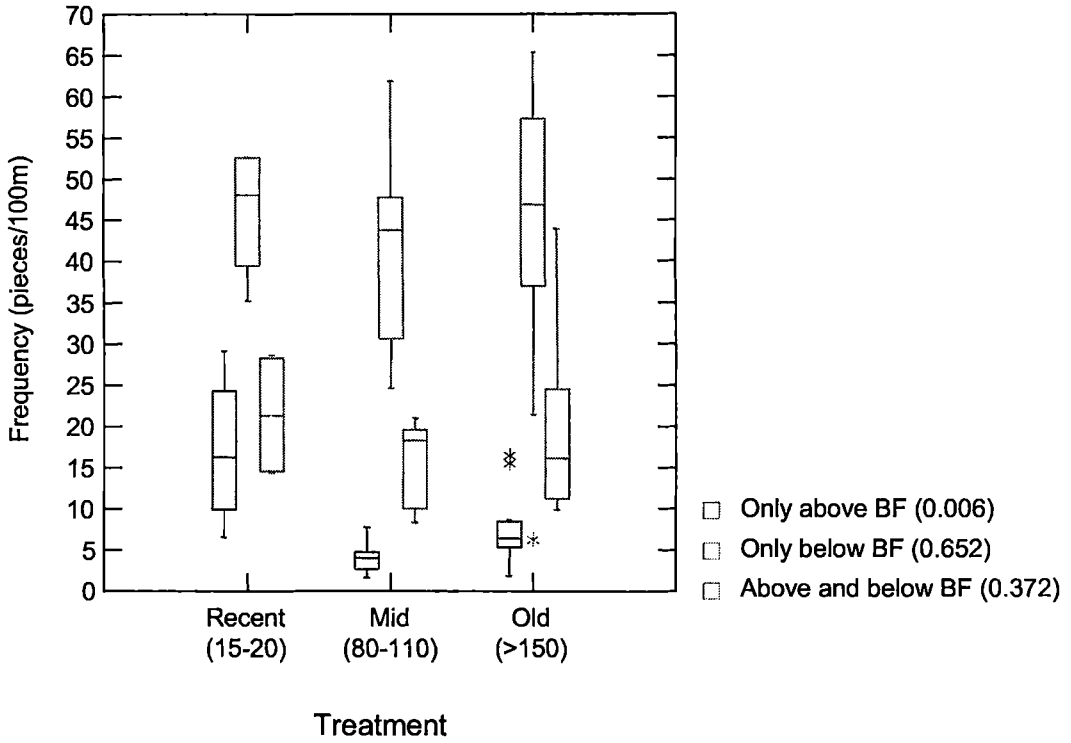


Figure 4. Box plots of the vertical position of wood within cross sections for data classified by time since riparian burn. *P*-values are shown in the legend. Values in parentheses on the *x*-axis represent the time since fire in years. Box plot features are: hinges- 1st and 3rd quartiles; whiskers- inner fences (top or bottom hinge plus/minus 1.5 times the interquartile range, or the extent of the data, whichever comes first); asterisk- data between inner and outer fences (hinge plus/minus 3 times the interquartile range); empty circle- data outside outer fence. BF indicates bank-full.

Embedment of wood

There is no significant difference between treatments in the amount of wood embedded in the bank or bed (Figure 5). There is, however, a significant difference in the amount of non-embedded wood. Recent and old treatments both have significantly more non-embedded wood than the mid treatment (P=0.052 and 0.072, respectively), while the former two are not statistically different from one another. The observed difference in the number of non-embedded

pieces probably reflects the amount of wood suspended above the bank-full channel (Figure 4), which by definition is not embedded. Consequently, the Figure 5 results are not an independent difference.

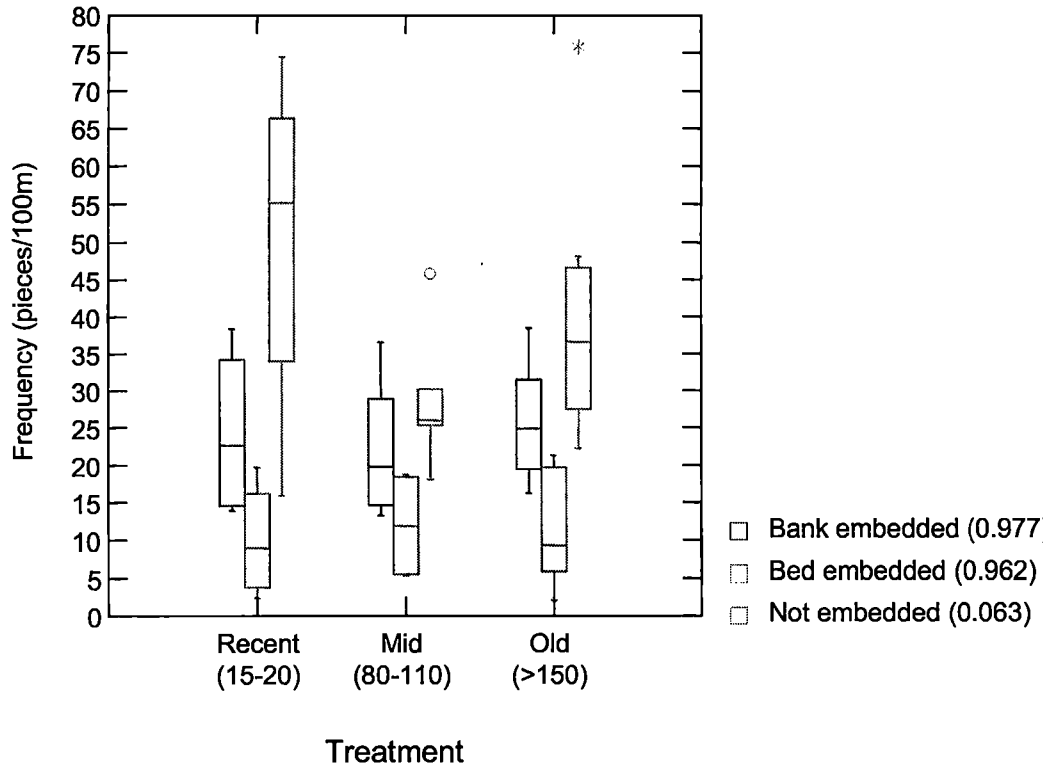


Figure 5. Box plots of wood embedment for data classified by time since riparian burn. *P*-values are shown in the legend. See Figure 4 caption for definition of box-plot symbols.

Wood frequency

The observed pattern in total wood frequency across treatments is similar to results of recent wood recruitment models (e.g., Benda and Sias, 2003), with the greatest frequency of wood occurring after fire (recent), the least during forest recovery (mid), and a moderate amount during old seral stages (old) (Figure 6). However, the observed differences in total wood frequency are not significant (P=0.112), nor are the differences in the frequency of functional

wood (P=0.921). The only significant difference is the frequency of non-functional wood, with more non-functional wood in the recent treatment than in the mid and old treatments (P=0.015 and 0.095, respectively). Consequently, the pattern of changes in total wood across treatments is largely driven by changes in non-functional wood at the study sites.

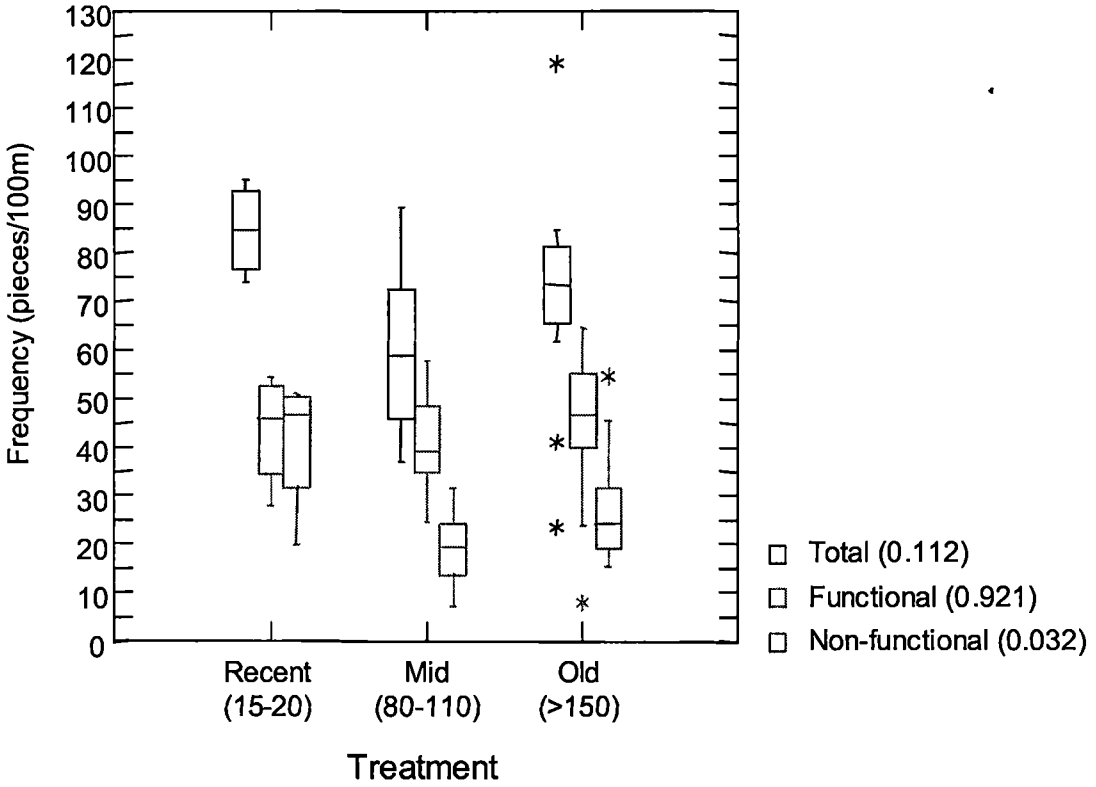


Figure 6. Box plots of wood frequency for the data classified by time since riparian burn. P-values are shown in the legend. See Figure 4 caption for definition of box-plot symbols.

Wood diameter

Wood diameter is not significantly different across treatments (P=0.354, Table 4); however, the observed variability was large enough to have physical or biological importance. Q-Q plots are a non-statistical approach for examining these differences. Figure 7 shows that the

mid treatment has a smaller range of diameters than the recent and old treatments, which tend to be similar to one another. The mid treatment has a smaller range of wood diameters, with pieces typically less than about 50 cm in diameter. In contrast, the recent and old treatments both have maximum diameters near 100 cm and several observations greater than 50 cm. However, these differences in wood diameter do not cause any significant differences in channel characteristics (Table 5). Differences in diameter of this magnitude might be important in larger channels, where larger pieces of wood are required to affect channel form (Bilby and Ward, 1989; Montgomery et al., 2003).

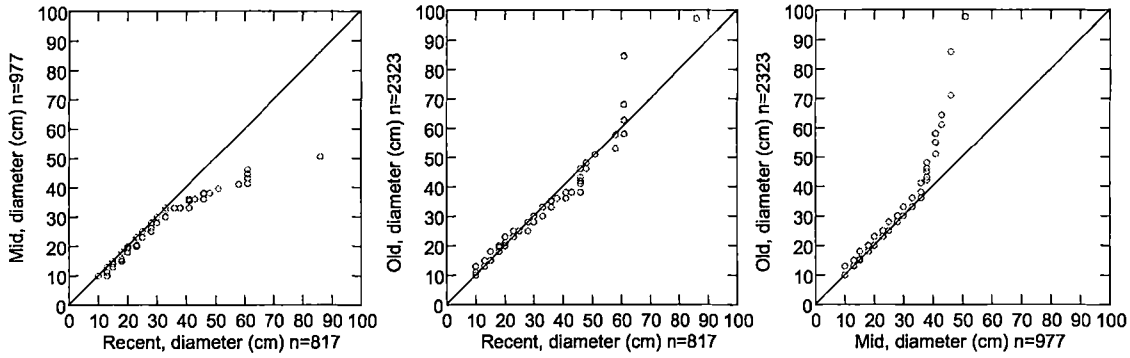


Figure 7. *Q-Q* plots of wood diameters (cm) for the data classified by time since riparian burn. The number of observations (*n*) is included on each axis label, with observations pooled per treatment.

Wood distribution

Recent studies show that riparian trees tend to fall towards streams (Sobota, 2003). However, less is know about the spatial distribution of wood within the channel, which may have relevance for processes bringing trees into channels, particularly where fluvial transport of wood is minor. Random events are based on Poisson processes, and the spacing between Poisson distributed events or objects is given by an exponential distribution (Haan, 1977). Therefore, trees that randomly fall into a stream should have spacings represented by an exponential

distribution. A chi-squared test was used to compare observed wood spacing to that of an exponential distribution.

Twenty of the 23 reaches studied had wood distributions significantly different from an exponential distribution ($P<0.05$, χ^2 test). Reaches with exponential wood distribution (Figure 8) had fewer pieces in the smallest spacing class (0-1.0 m), or less clumping, than reaches with non-exponential wood spacing (Figure 9). The non-exponential data show a greater number of pieces closer to one another (0-1 m), fewer pieces with moderate spacing (1-4 m), and more pieces with large spacing (> 4 m) than would be predicted by an exponential distribution (Figure 9). This may indicate a separation of scales with some process yielding clumping at scales less than 1 m and others at greater than 4 m. Clumping of wood may be due to multiple trees falling in the same location, with one tree knocking over others, by a localized wind burst, localized disease, localized undercut banks, or other spatially coherent process. The formation of periodic wood jams via fluvial transport is likely precluded at these study sites due to their low stream slopes and relatively narrow channel widths, allowing transport of only very small wood. Therefore, the observed spatial clumping of wood suggests that wood was not recruited to the stream based on individual random tree falls. These results agree with those of Robison and Beschta (1990), who found non-systematic (or discontinuous) spacing of wood in undisturbed southeast Alaska streams of similar size to these sites. At the Idaho sites, all non-exponential distributions appeared to be better fit by a negative binomial distribution. Results herein show that wood spacing is not random and suggest that models based on or derived from consideration of individual tree fall need to consider interaction between individual trees when estimating total wood loading (Gregory et al., 2003).

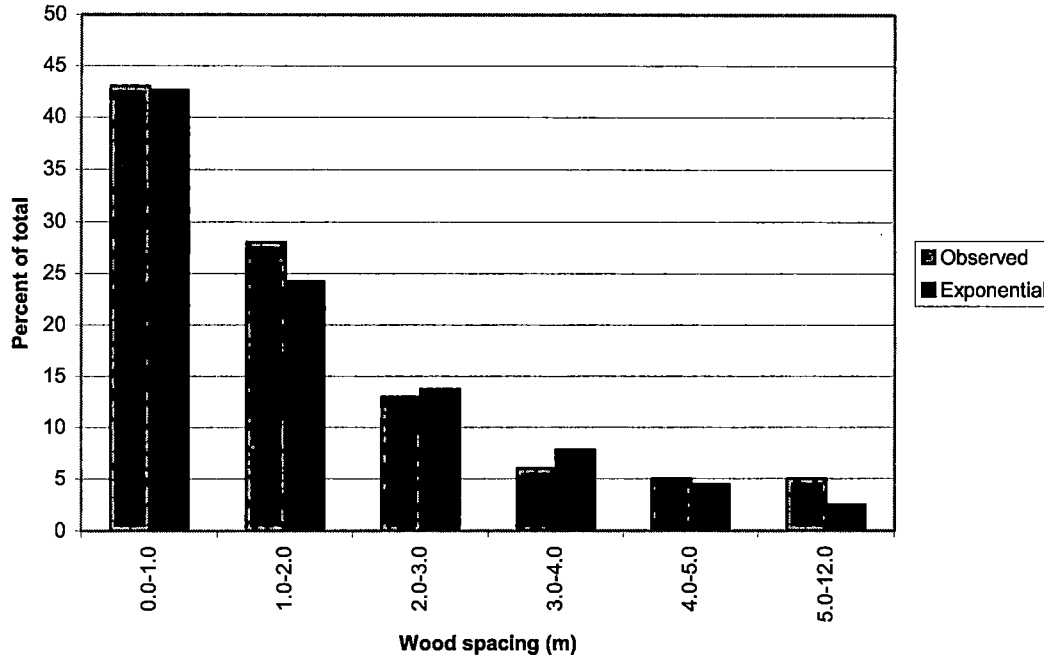


Figure 8. Example of a stream with an exponential distribution of wood spacing, Van Buren Creek.

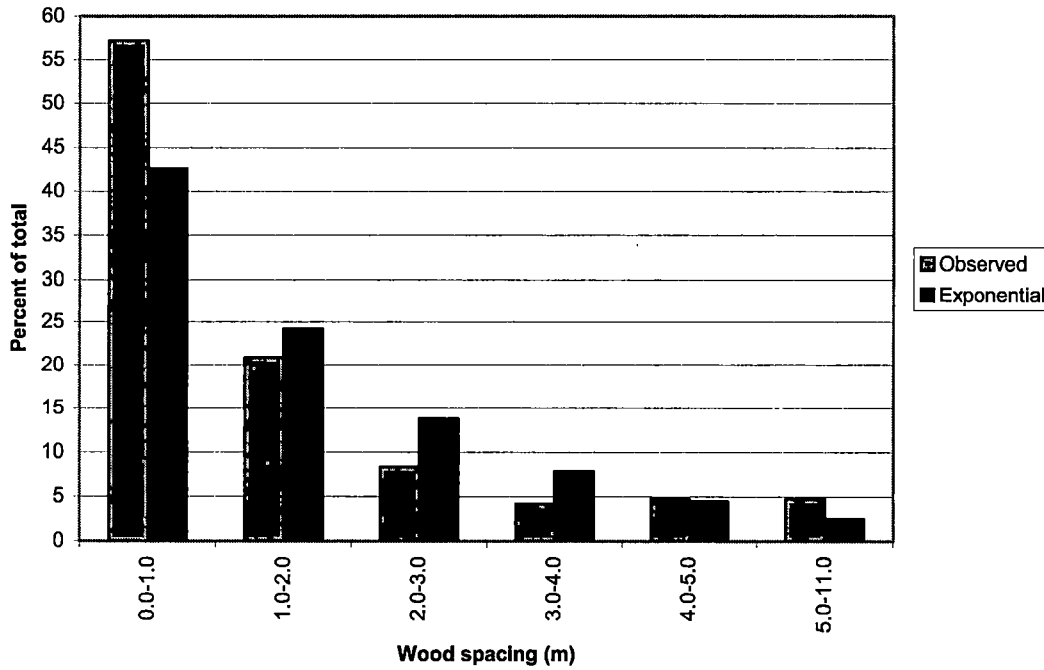


Figure 9. Example of a stream with non-exponential distribution of wood spacing and some clumping of wood, Otterson Creek.

Wood decay and timing of recruitment

There are no significant differences in wood decay classes for riparian and synchronous burn classifications of the data (P>0.261, MRPP, not shown in Table 4). To better understand the effects of fire on riparian recruitment of wood, we can define the following four sources of input: 1) carry over (wood that was in the stream or on the floodplain prior to fire), 2) fire mortality (wood that toppled into the stream after being burned), 3) remnant stand (recruitment from the unburned portion of the riparian forest), or 4) new stand (input from the fire-regenerated stand) (Spies et al., 1988). As discussed in previous sections, fluvial transport of wood is unlikely at the study sites and, therefore, upstream input is not considered as a source of wood.

Wood decay classes (Appendix A5) and degree of burial were used to estimate sources of wood input in each treatment (Figure 10). The base (white segment) of each bar represents decay classes 3 and 4 (Appendix A5), or "old wood". The top of each bar (gray segment) represents unburied wood having decay classes 1 or 2 (Appendix A5), or "new wood". At recently burned sites, fire mortality and the remnant stand were the two primary sources of new wood (decay classes 1 and 2), while decay classes 3 and 4 better represent carry-over wood. In the mid treatment, new and remnant stands can provide new wood (decay classes 1 and 2), and old wood is derived from fire mortality, carry-over wood, or the remnant stand. The remnant stand may provide new or old wood to the mid and old treatments because it may have a wide range of tree ages. In the old treatment, it is less likely that fire mortality and carry over contribute to the amount of old wood present in the stream.

Although decay classes are not uniquely related to specific wood sources over time and across treatments, the amount of new wood in the recent treatment is relatively small compared

to the amount of old wood, or carry over (Figure 10). This suggests that carry-over wood may play an important role in supplying the mid-treatment channels with wood during the post-fire lag in recruitment while the riparian forest is regrowing. However, as will be discussed in later sections, fire-related wood stored in suspension is another important source of future functional wood that may buffer fire-related disruption of riparian recruitment. The wood stored in suspension may have been derived, in part, from carry-over, fire mortality or the remnant stand. Hence, all of these sources of wood may also be important for supplying wood to mid-treatment channels.

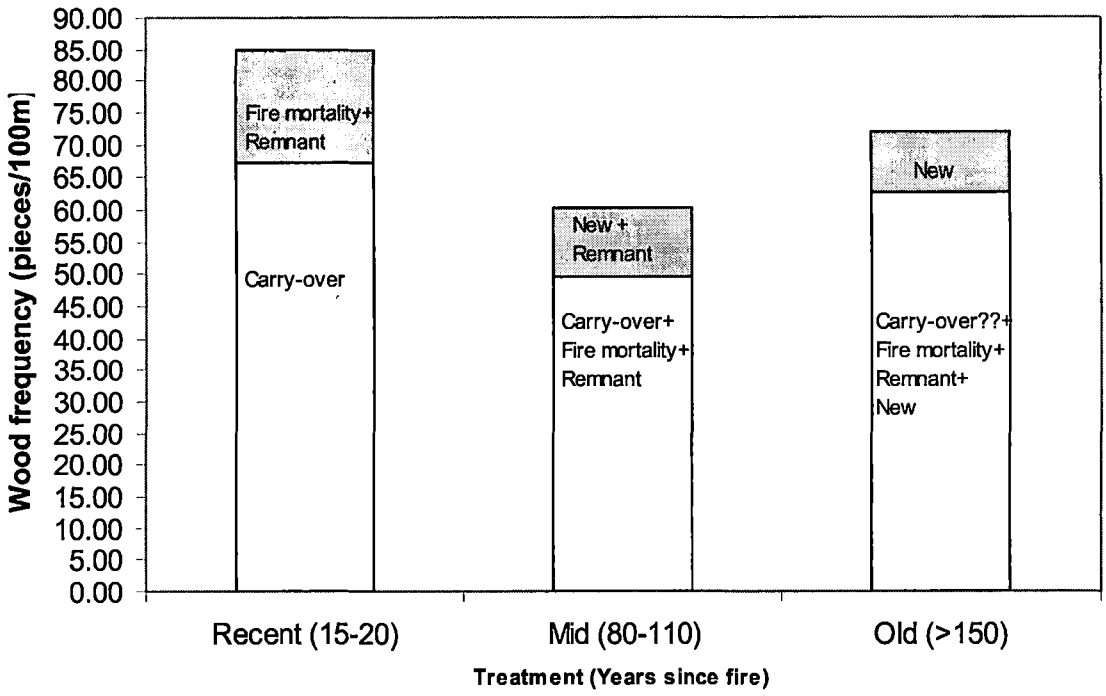


Figure 10. Mean values of wood sources over time for data classified by time since riparian burn. The base of each bar represents decay classes 3 and 4 (Appendix 5), or "old wood". The gray portions represent decay classes 1 and 2 (Appendix 5), or "new wood". The likely wood source(s) are indicated within each box.

Channel characteristics

Sediment

Median surface grain size (D_{50}) was not significantly different between treatments (P=0.741, Table 5). However, the treatment means show substantial differences on the order of 43 % (Table 5a), which may have biological importance in terms of the availability of suitable spawning gravels for salmonids (e.g., Kondolf and Wolman, 1993; Buffington et al., 2004). *Q-Q* plots are used to further examine characteristics of the full grain-size distributions (rather than just the median size) for each treatment. The basin burn classification of the data is presented here to analyze potential grain-size response to post-fire alterations of sediment supply and hydrology. In this analysis, grain sizes were limited to those smaller than 256 mm (boulders) because larger grain sizes at the study sites are less mobile, and therefore less responsive to changes in hydrology. Larger grain sizes are also less responsive to changes in sediment supply, as it would require a greater amount of fine sediment to bury these large grains. *Q-Q* analysis shows that the mid treatment has a slightly finer distribution than the recent and old treatments (Figure 11). In particular, the shift in treatment means is primarily due to a greater abundance of particles less than 15 mm in the mid treatment. These results also may have biological importance, in that increases in the abundance of fine material can be detrimental to aquatic species (e.g., Bjornn and Reiser, 1991).

In addition, the proportion of dominant substrate (Appendix A4) at the points of maximum pool depth and riffle crest were not significantly different between treatments for all burn classifications (P>0.05, χ^2 test of equality of proportions) (Figures 12 and 13). The point of maximum pool depth is expected to be the location of maximum scour in high flows, and a likely place for fine sedimentation at low flows. Riffle crests can be a local point of aggradation that is

related to scour characteristics of the pool immediately upstream. The lack of difference in the substrate found at these locations suggests that high and low flow sedimentation is similar between treatments. These results are of particular importance to salmonid spawning, as salmon and trout often prefer to spawn near the riffle crest (i.e., pool tail-outs) and require clean gravels (<20% of the grain-size distribution finer than 6 mm) (Bjornn and Reiser, 1991; Baxter and Hauer, 2000).

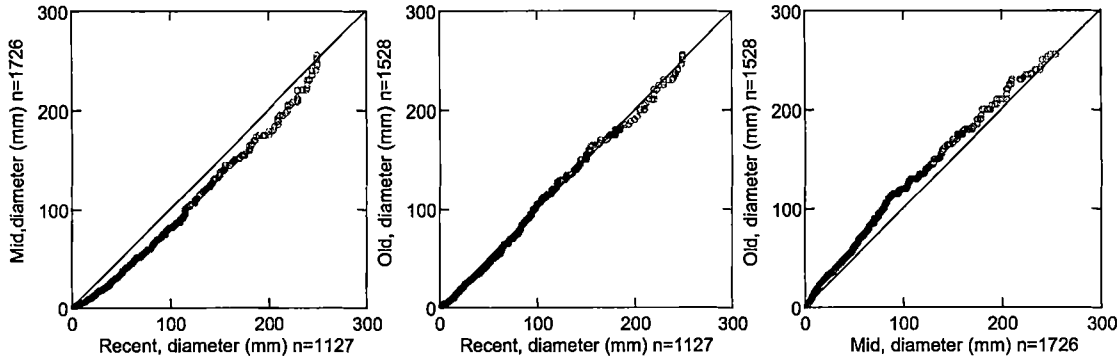


Figure 11. *Q-Q* plots of surface grain sizes smaller than 256 mm for data classified by time since basin burn. The number of observations (*n*) is reported on each axis label, with observations pooled per treatment.

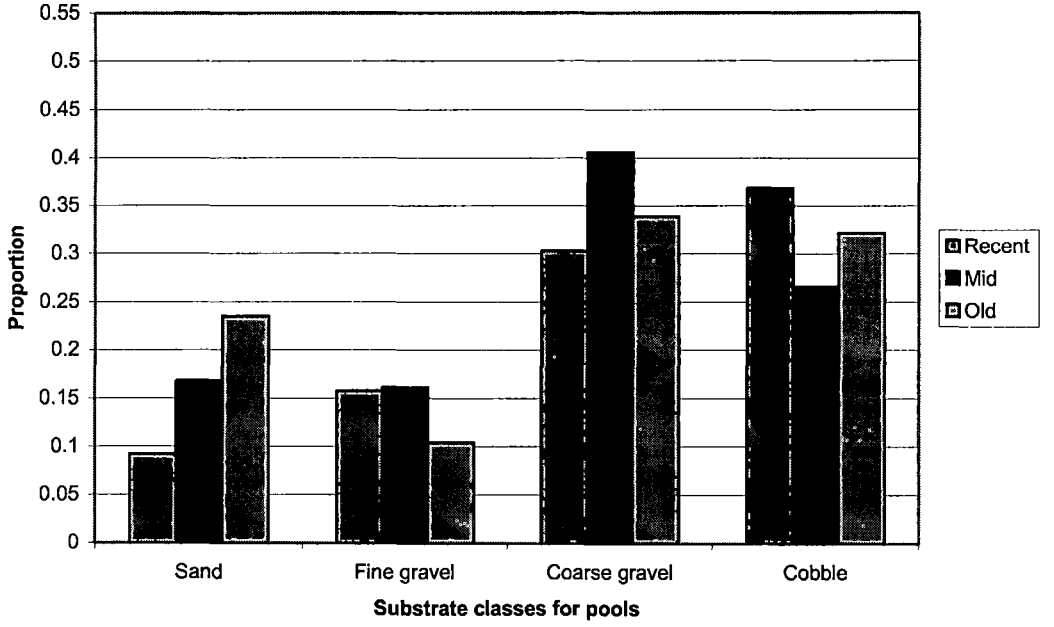


Figure 12. Dominant substrate at pool bottoms for data classified by time since basin burn. A χ^2 test of equality of proportions finds no significant difference between treatments (P>0.05). Where, sand is <2 mm, fine gravel is 2-8 mm, coarse gravel is 8-64 mm, and cobble is 64-256 mm.

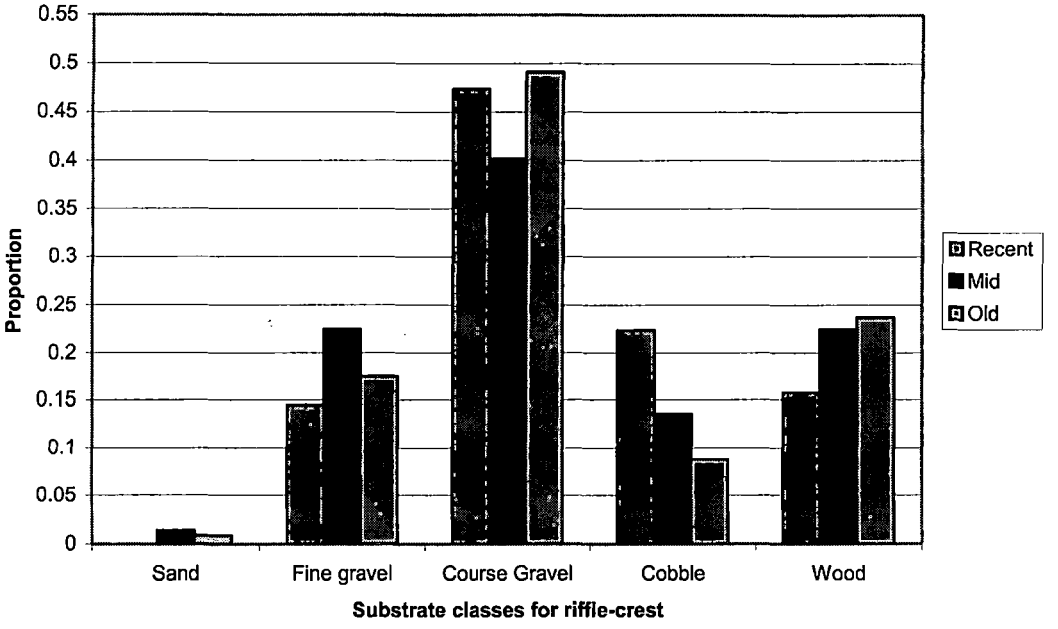


Figure 13. Dominant substrate at riffle crests for data classified by time since basin burn. A χ^2 test of equality of proportions finds no significant difference between treatments (P>0.05). Where, sand is <2 mm, fine gravel is 2-8 mm, coarse gravel is 8-64 mm, and cobble is 64-256 mm.

Pool spacing & pool type

The riparian and synchronous burn classifications of the data are used here to examine the effects of locally-supplied wood in forming pools during riparian forest succession; as discussed earlier, it is hypothesized that little fluvial transport of wood occurs at the study sites and that most of the in-channel wood is supplied from the local riparian forest. No significant differences in pool spacing were observed across the different burn classifications (P=0.702, Table 5), but pool spacing is an important measure of habitat quality, and so is further examined here. Pool spacing was normalized by the average active channel width, as opposed to the bank-full width, because active channel widths could be measured with more confidence than bank-full widths.

Q-Q plots reveal that distributions of pool spacing are similar among treatments up to values of about 7 active channel widths, beyond which the recent and old treatments tend to have a greater number of more widely spaced pools than the mid treatment (Figure 14). Again showing that the mid treatment has different characteristics than the recent and old treatments. However, because these observations make up a small proportion of the entire data set this difference is not significant according to the MRPP analysis. The observed values of wood frequency and pool spacing for the Idaho study sites are within the range reported by Montgomery et al. (2003) for other western streams, but are most similar to their data for the southern Rockies and northern Cascade mountain ranges.

Results also show that there is no significant difference in the total frequency of pools (P=0.568), the frequency of self-formed and boulder-forced pools (P=0.748), or the frequency of wood-forced pools (P=0.598) across the riparian and synchronous burn classifications (Figure 15). Self-formed and boulder-forced pools are combined in this analysis because we did not differentiate between the two in the field.

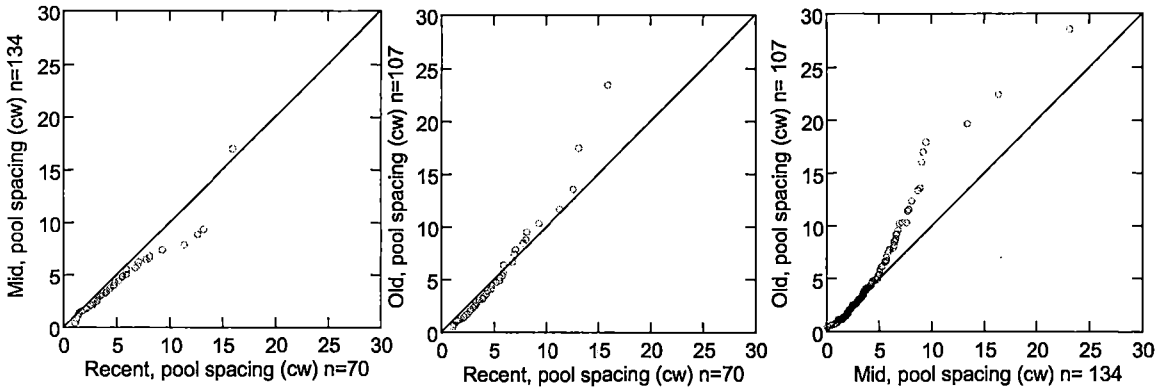


Figure 14. *Q-Q* plots of pool spacing (expressed in active channel widths, cw) for data classified by time since riparian burn. Results shown here are typical of the other burn classifications. The number of observations (*n*) is indicated on each axis label, with data pooled per treatment.

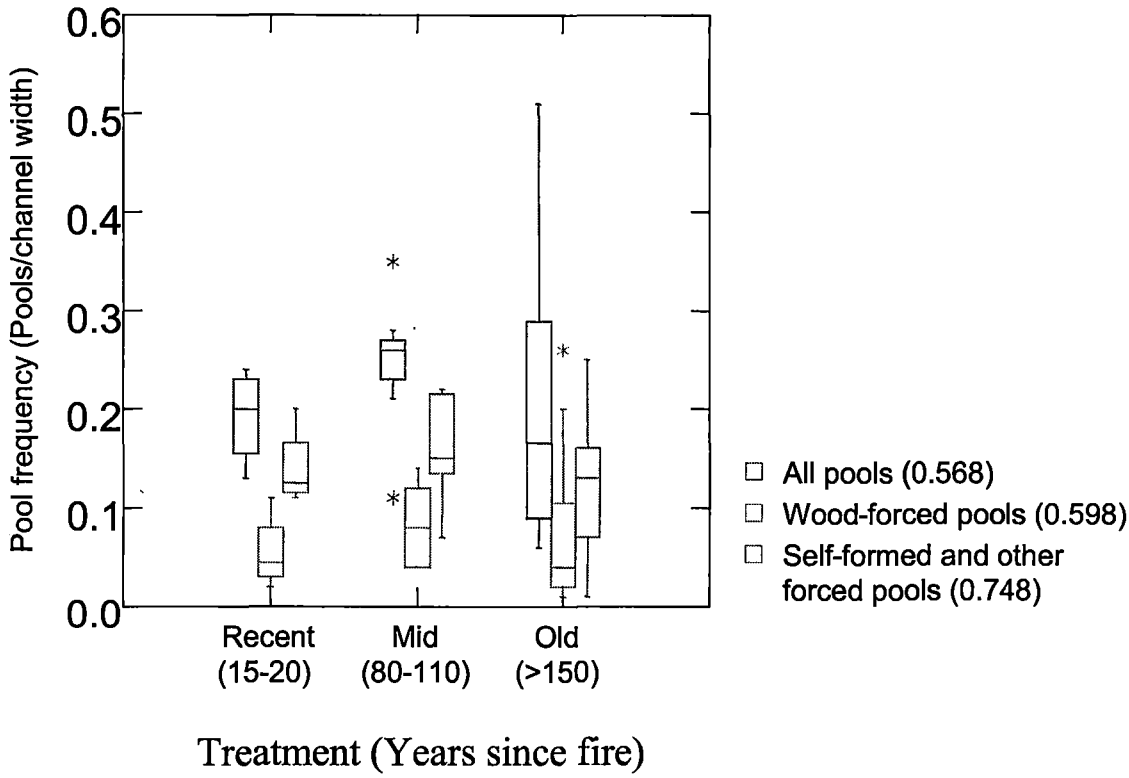


Figure 15. Box plots of pool frequency for data classified by time since riparian burn. *P*-values are shown in the legend. See Figure 4 caption for definition of box-plot symbols.

Maximum residual depth between cross sections

There is no significant difference in maximum residual depth between cross sections for data classified by time since basin burn (P=0.909), riparian burn (P=0.327), or synchronous burn (P=0.565) (Table 5). Nevertheless, maximum residual depth is an important measure of habitat cover and, therefore, is further examined. Figure 16 shows results for maximum residual depths for data classified by time since basin burn. Again, the basin burn classification of the data is presented, as it is typical of the other burn classifications. These data show that maximum residual depths are most similar in the old and mid treatments, while the recent treatment tends to have relatively shallow residual depths. Consequently, channels recently impacted by wildfire may have somewhat less habitat cover (smaller residual depths), but the differences between treatments are not statistically significant according to the MRRP analysis.

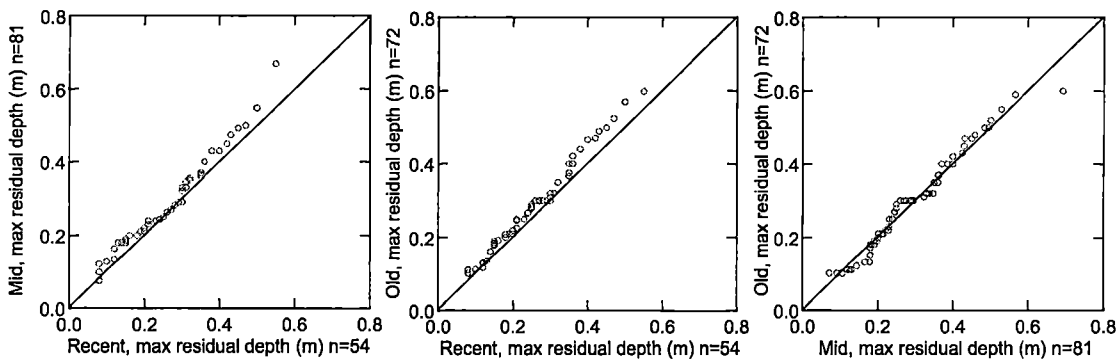


Figure 16. *Q-Q* plots of maximum residual depth between cross sections for data classified by time since basin burn. The number of observations (n) is included on each axis label, with data pooled per treatment.

DISCUSSION

Channel characteristics

The lack of significant differences in channel characteristics for the basin and synchronous burn classifications of the data suggests that fire-related alterations of hydrologic and sediment regimes did not have long-term (> 20 year) effects on the channel morphology of these reaches. Consequently, any changes in these regimes were either geomorphically insignificant or were short-lived, with the channel form recovering within 15-20 years (i.e., over time scales shorter than the smallest sampling period used in this study). For example, Potyondy and Hardy (1994) found that fine sediment introduced by wildfire was quickly winnowed from the streambed by flood flows, and that surface material recovered to pre-disturbance conditions within 2-3 years. The lack of significant differences in channel characteristics for time since basin burn (reaches where only the upland forest burned) is the least surprising, given the notion that fire-related effects on hydrologic and sediment regimes tend to be more short-lived than effects on the riparian forest and consequent wood recruitment to these channels (Minshall et al., 1989; Minshall and Brock, 1991). The lack of significant differences in channel characteristics for time since synchronous burn and time since riparian burn is more surprising, given that numerous studies have hypothesized that channel characteristics will change in concert with forest succession and altered characteristics of wood recruitment (e.g., Minshall, 1989; Beechie et al., 2000).

Wood characteristics

Significant differences in wood characteristics did not drive significant differences in channel characteristics for time since riparian burn or time since synchronous burn because there was little change in wood that affected channel hydraulics. Most of the wood input after fire is suspended above the channel because of small channel widths relative to wood lengths. The majority of riparian trees at the study sites are tall/long enough to easily bridge the channel for many fall directions, even if they break upon fall. Furthermore, the probability of fall breakage is likely to be low given the relatively short height of riparian trees (mean height = 21 m) (Sobota, 2003). Hence, we would expect to see a large percentage of recently recruited wood to be suspended above the channel (Van Sickle and Gregory, 1990; Robison and Beschta, 1990) and geomorphically ineffective for most flows.

When wood initially falls over an unconfined stream, the potential for it to fall below bank-full where it can interact with the stream may be related to the ratio of stream width (w) to length of input wood (L), termed here the functional recruitment ratio ($FR=w/L$). Figure 17 is a cartoon that compares a high FR ratio to a low FR ratio, where the wood length is constant for each case, but the stream width is varied. Wood that is suspended over the channel may eventually enter the channel due to decay and breakage, or due to fluvial undercutting of the supporting bank. However, Murphy and Koski (1989) found that some wood in southeast Alaskan streams may remain suspended over the channel as long as 100 years after recruitment from the riparian forest. Consequently, low FR values and, subsequent, suspension of wood over the channel could significantly slow the recruitment of wood to geomorphically effective locations, buffering the effects of post-fire increases in riparian input of wood (Swanson and Lienkaemper, 1978).

Figure 3 supports this expectation, showing that the recent treatment has significantly more wood pieces above bank-full than both the mid and old treatments, and that there is no difference between treatments in the number of pieces below bank-full and both above and below bank-full. Hence, suspension appears to buffer the effects of greater post-fire input of wood from the riparian zone. In similar streams, Robinson et al. (2005) found 5 times more wood in streams recently burned, compared to unburned streams. They also found that a significant portion of recently recruited wood did not directly interact with the channel, and reported that 80 percent of the wood bridged these burned streams.

Within the context of this study, the FR ratio addresses the problem of wood entry into the channel. However, once wood enters the channel its geomorphic effectiveness depends on the size of the wood relative to the size of the channel (e.g., Montgomery et al., 2003).

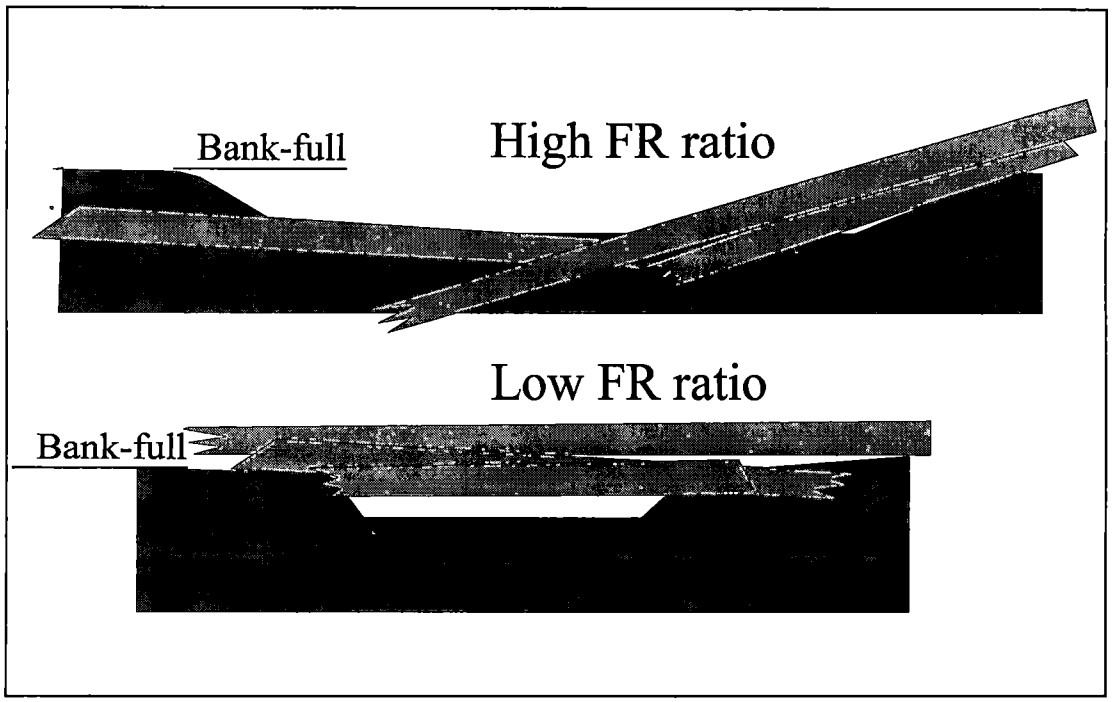


Figure 17. Cartoon depicting generalized *FR* ratios.

The greater number of pieces of wood above bank-full from fire-toppling in the recent treatment likely explains the higher numbers of non-functional wood in that treatment (Figure 6) and the greater abundance of wood not embedded in the channel bed and banks (Figure 5). To examine this issue, the MRPP analysis was re-run after removing the recently recruited pieces of wood (unsubmerged pieces in decay classes 1 and 2, Appendix 5) that were located above bank-full in the recent treatment. This reanalysis removes the differences in non-functional wood and non-embedded wood across the treatments ($P > 0.10$). Hence, there is really only one, independent, significant difference in the wood characteristics at these sites: the number of pieces only above bank-full. The numbers of non-embedded and non-functional pieces are not independent factors, but rather are functions of the number of pieces above bank-full.

It was also found that the frequency of functional wood does not vary statistically among reaches. This suggests a stable supply of functional wood over time despite wildfire disturbance. To better understand this finding we can consider wood sources and the mechanisms that supply wood from these sources to the stream. Potential stores of wood include pieces suspended above bank-full, wood on the floodplain, wood buried below the channel and wood buried in the banks (Hyatt and Naiman, 2001; Montgomery and Abbe, 2006). Wood suspended above the channel could be accessed through decay and breakage into the channel, through channel migration that undercuts a supporting bank and causes suspended wood to fall into the channel, or by the channel aggrading up to the wood. Branches hanging from a suspended piece of wood may slow the flow or trap other floating debris, causing the channel to locally aggrade and either erode one bank, undercutting the suspended piece of wood, or partially bury the wood, creating a stepped profile. Lateral migration or, in more extreme cases, channel avulsion may cause the stream to capture wood located on the floodplain or buried within the alluvial valley fill. Finally, should

the channel begin to incise, it may interact with more buried wood (e.g., Lisle, 1986). Roughly half of the wood in the mid and old treatments was embedded, implying origins in buried wood (Table 4), and suggesting active movement of the channel that both buries and exhumes wood. Frequent over-bank sedimentation may also be important to burial. Rapid burial by channel movement and floodplain sedimentation is important to creating large stores of wood because preservation of wood requires it to be buried or submerged soon after it falls. The abundance of functional wood within the channel may also be modulated by low rates of wood decay and mechanical wearing due to low channel slopes and low water and air temperatures (Bilby, 2003).

It was found that the majority of wood in the recent treatments was carry-over wood from the antecedent stand (Figure 10). This suggests that carry-over wood from the recent treatment may play a significant role in supplying wood to these streams during forest reestablishment. Carry-over wood may result from a low mechanical wearing/decay rate of in-channel wood or come from one of the stores discussed above. Studies have shown that buried wood decays extremely slowly and may persist for hundreds, or even thousands, of years (Nanson et al., 1995; Hyatt and Naiman, 2001; Abbe and Montgomery, 2006). Wood submerged or buried in the floodplain maintains structural integrity over time. If such wood is exposed to surface discharge, as the channel migrates laterally or incises, it can be relatively resistant to stress and abrasion. These pieces may act as a rigid structure maintaining channel form and moderating wood abundance (e.g., Montgomery and Abbe, 2006) by buffering the overall decrease in wood amount during times of net sediment transport and incision as a stream exposes buried wood.

Although, one might expect to see more pieces of wood associated with streams after fire-toppling and less during times of forest reestablishment, it is hypothesized that the study sites are characterized by buffering mechanisms (wood stored in suspension and buried wood) that

maintain a relatively constant amount of geomorphically effective wood over time scales of forest succession. In early seral stages (recent treatment) wood may be trapped above bank-full due to low *FR* ratios, modulating the impact of post-fire pulses of wood input to the stream. As for mid-seral stages (mid treatment), buffering mechanisms may be exhumation of wood or the incorporation of suspended wood into the stream, thereby supplying wood during the lag time in riparian recruitment. Moreover, the lack of significant geomorphic differences between treatments for all burn classifications indicates that the dotted blue line in Figure 1 best represents the response trajectory of habitat quality for these reaches.

Management implications

The stability of small, low- to moderate-gradient streams with wide valleys may have implications for population dynamics of fishes in dynamic landscapes. Ensuring connectivity between these stream types and ones more prone to disturbance may be of critical importance to persistence of fishes by providing potential refugia from disturbance, or creating population sources for recolonization of catastrophically disturbed areas.

The identification of stable stream habitats may also help to prioritize fuel treatment locations at the watershed scale. For example, fuels reduction treatments meant to "protect" this stream type may not be needed given its lack of response to fire disturbance. Furthermore, periodic input of fire-toppled wood that is stored in suspension and slowly input to the channel over time may be an important part of maintaining functional wood and channel stability in this stream type. Consequently, fire management that disrupts this process may have a negative impact on channel stability and aquatic habitat quality.

Reaches similar to those studied here, but that were subject to anthropogenic disturbance, such as "stream cleaning" or riparian logging, may be good locations for channel restoration efforts, as habitat improvement structures should be stable over long time periods. Structures placed in such sites would likely be stable and persistent because they are decoupled from hillslope disturbances, have low potential for fluvial transport due to low channel slopes, and may have low decay/mechanical wearing rates. However, if the buffering mechanisms (wood trapped above bank-full and floodplain storage of wood) are no longer present due to the anthropogenic disturbance, the channel may be less stable than the sites examined in this study.

CONCLUSIONS

The lack of morphologic variability over time since major fires implies that wildfire disturbance does not have a major long-term effect on channels of this stream type, suggesting that low- to moderate-gradient, unconfined channels can act as relatively stable, potentially productive, refugia relative to larger-scale disturbances occurring in a basin. Response to post-fire disturbances depends on channel type and position in the river network (connection to hillslopes and sequence of upstream channels and their ability to transmit disturbances (Montgomery and Buffington, 1998; Rice, 1994). The channels examined in this study were buffered from direct post-fire debris-flow impacts because of low stream gradients and wide alluvial valleys (decoupling the channel from direct hillslope inputs and allowing debris flows to spread out and deposit upstream from the study sites). These channels exhibit characteristics of response reaches (unconfined, alluvial valley fill, low slopes) (Montgomery and Buffington, 1998), yet results indicate that the study sites are relatively stable and morphologically unresponsive to wildfire disturbance. However, response may have occurred over shorter time-

scales than those examined in this study (i.e., less than 15 years after fire). Given that this study focuses on a single stream type, additional studies are needed in other stream types and geomorphic settings to examine variability in channel changes after wildfire disturbance. Compilation of such studies would greatly assist in development of risk-assessment models for stream and riparian ecosystem response to wildfire and forest management. Future studies of this nature should focus on *FR* ratios, decay/mechanical wearing rates, and wood sources and budgets (including buried wood) to gain a better understanding of mechanisms that influence functional wood supply.

Although this study focused on statistical differences between treatments, it is also important to consider physical and biological relevance of observed differences. While some differences were not statistically significant, it is possible that the absolute magnitudes of the difference are great enough to have physical or biological relevance. For example, if we consider D_{50} values observed in the recent and mid treatments for time since basin burn, we see that D_{50} values for the mid treatment are 43% smaller than the recent treatment. Despite a lack of statistical significance, differences such as this may be important biologically in terms of the availability of spawning gravel or rearing habitat for specific species (Kondolf and Wolman, 1993; Buffington et al., 2004), and may be an important factor when evaluating the effect of fire-related response on aquatic organisms.

LITERATURE CITED

Agee, J. K. 1993. Fire ecology of pacific northwest forests. Island Press. Washington, D.C.

Baxter, C.V., and H.R., Hauer. 2000. Geomorphology, hyporheic exchange, and spawning selection by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57: 1470-1481.

Beechie, T.J., G. Pess, P. Kennard, R.E. Bilby, and S. Bolton. 2000. Modeling recovery rates and pathways for woody debris recruitment in northwestern Washington streams. North American Journal of Fisheries Management 20:436-452.

Benda, L. E., and T. Dunne. 1997a. Stochastic forcing of sediment supply to the channel network from landsliding and debris flow. Water Resources Research 33:2849-2863.

Benda, L. E., and T. Dunne. 1997b. Stochastic forcing of sediment routing and storage in channel networks. Water Resources Research 33:2865-2880.

Benda, L. E., D.J. Miller, T. Dunne, G.H. Reeves, and J.K. Agee. 1998. Dynamic landscape systems. *in* R. J. Naiman, and R.E. Bilby, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer Verlag, New York.

Benda, L. E., and J. C. Sias. 2003. A quantitative framework for evaluating the mass balance of instream organic debris. Forest Ecology and Management 172:1-16.

Benda, L. E., D. Miller, P. Bigelow, and K. Andras. 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. Forest Ecology and Management 6240:1-15.

Berry, K. J., and P.W. Mielke. 1983. Computation of finite population parameters and approximate probability values for multi-response permutation procedures (MRPP). Communication in Statistics - Simulation and Computation 12:83-107.

Bilby, R.E., J.W. Ward. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. Transactions of American Fisheries Society 118:368-378.

Bilby, R.E. 2003. Decomposition and nutrient dynamics of wood in streams and rivers. Pages 135-148. *in* S.V. Gregory, K.L. Boyer, and A.M. Gurnell, editors. The ecology and management of wood in world rivers. American Fisheries Society Symposium 37. Bethesda, Maryland.

Bisson P.A., B.E. Rieman, C. Luce, P.F. Hessburg, D.C. Lee, J.L. Kershner, G.H. Reeves, R.E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management 178:213-229.

Bjornn, T.C., and D.W. Reiser. 1991. Habitat Requirements of Salmonids in Streams. Pages 83-138. *in* W.R. Meehan, editor. Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. American Fisheries Society Special Publication 19, Bethesda, Maryland.

Buffington, J.M., D.R. Montgomery. 1999. Effects of hydraulic roughness on surface textures of gravel-bed rivers. Water Resources Research 35:3507-3521.

Buffington, J. M., D. R. Montgomery, and H. M. Greenberg. 2004. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. Canadian Journal of Fisheries and Aquatic Sciences 61:2085-2096.

Dilworth, J.R., J.F. Bell. 1981. Variable plot cruising. Pages 259-368. *in* Log Scaling and Timber Cruising. Oregon State University Bookstores. Corvallis, Oregon.

Dunham J.B., M.K. Young, R.E. Gresswell, B.E. Rieman. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. Forest Ecology and Management 178:183-196.

Gregory, S. V., K.L, Boyer, and A.M. Gurnell, editors. 2003. The ecology and management of wood in world rivers. American Fisheries Society. Bethesda, Maryland.

Haan, C.T. 1977. Statistical methods in hydrology. Iowa State University Press. Ames, Iowa.

Harmon, M. E., and 12 others. 1986. Ecology of coarse woody debris in temperate ecosystems. Bioscience 15:133-302.

Horton, R. E. 1945. Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. Bulletin of the Geological Society of America 56:275-370.

Hyatt, T.L., and R.J. Naiman. 2001. The residence time of large woody debris in the Queets River, Washington, USA. Ecological Applications 11:191-202.

Iyer, H. K., K.J. Berry, and P.W. Mielke. 1983. Computation of finite population parameters and approximate probability values for multi-response randomized block permutation procedures (MRBP). Communication in Statistics - Simulation and Computation 12:479-499.

Kondolf, G.M., and M.G. Wolman. 1993. The sizes of salmonid spawning gravels. Water Resources Research 29: 2275-2285.

Lisle, T. E. 1987. Using residual depths to monitor pool depths independently from discharge. Research Note PSW-394, USDA Forest Service, Albany, CA.

Meyer, G. A., S.G. Wells, R.C. Balling Jr., and A.J.T. Jull. 1992. Response of alluvial systems to fire and climate change in Yellowstone National Park. Nature (London) 357:147-150.

Meyer, G. A., S.G. Wells, and A.J.T. Jull. 1995. Fire and alluvial chronology in Yellowstone National Park: climatic and intrinsic controls on Holocene geomorphic processes. Geological Society of America Bulletin 107:1211-1230.

Mielke, P. W., K.J. Berry, and G.W. Brier. 1981. Application of multi-response permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. Monthly Weather Review 109:120-126.

Mielke, P. W., and K.J. Berry. 1982. An extended class of permutation techniques for matched pairs. Communications in Statistics-Theory and Methods A11:1197-1207.

Mielke, P. W., K.J. Berry, and J.G. Medina. 1982. Climax I and II: distortion resistant residual analysis. Journal of Applied Meteorology 21:788-792.

Mielke, P. W., and K.J. Berry. 1983. Asymptotic clarifications, generalizations, and concerns regarding an extended class of matched pairs tests based on powers of ranks. Psychometrika 48:183-485.

Mielke, P. W. 1984. Meteorological applications of permutation techniques based on distance functions. North-Holland Publishing, Amsterdam. The Netherlands.

Miller, D., C. Luce, and L.E. Benda. 2003. Time, space, and episodicity of physical disturbance in streams. Forest Ecology and Management 178:121-140.

Minshall, G. W., J.T. Brock, and J.D. Varley. 1989. A temporal perspective shows that aquatic recovery parallels forest succession Bioscience 39:707-715.

Minshall, G.W., J.T. Brock. 1991. Observed and anticipated effects of forest fire on Yellowstone stream ecosystems. *in* R.B. Keiter, and M.S. Boyce, editors. Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press. New Haven, Connecticut.

Montgomery, D. R., and J.M. Buffington. 1997. Channel reach morphology in mountain drainage basins. Geologic Society of American Bulletin 109:596-611.

Montgomery, D.R., and J.M. Buffington. 1998. Channel processes, classification, and response. Pages 13-42. *in* R., Naiman, and R. Bilby, Editors. River ecology and management. Springer-Verlag New York, Inc.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of American Water Resources Association 35:397-410.

Montgomery, D. R., B.D. Collins, J. M. Buffington, and T. B. Abbe. 2003. Geomorphic effects of wood in rivers. Pages 21-48. *in* S.V. Gregory, K.L. Boyer, and A.M. Gurnell, editors. The ecology and management of wood in world rivers. American Fisheries Society, Symposium 37. Bethesda, Maryland.

Moody, J. A., and D.A. Martin. 2001. Post-fire, rainfall intensity--peak discharge relations for three mountainous watersheds in the western USA. Hydrologic Processes 15:2981-2993.

Morgan, P., S.C., Bunting, A.E. Black, T. Merrill, and S. Barrett. 1996. Fire regimes in the interior Columbia River Basin: past and present. Final report for RJVA-INT-94913: Coarse-scale classification and mapping of disturbance regimes in the Columbia River Basin. Intermountain Research Station. Missoula, MT

Murphy, M.L., and K.V. Koski. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. North American Journal of Fisheries Management 9:427-436.

Nanson, G.C., M. Barbetti, and G. Taylor. 1995. River stabilization due to changing climate and vegetation during the late Quaternary in western Tasmania, Australia. Geomorphology 13:145-158.

Potyondy, J.P., and T. Hardy. 1994. Use of pebble counts to evaluate fine sediment increase in stream channels. Water Resources Bulletin 30:509-520.

Rieman, B.E., D. Lee, D. Burns, R. Gresswell, M. Young, R. Stowell, P. Howell. 2003. Status of native fishes in the Western United States and issues for fire and fuels management. Forest Ecology and Management. 178(1-2):19-212.

Reeves, G. H., L.E. Benda, K.M. Burnett, P.A. Bisson, and J.R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionary significant units of anadromous salmonids in the Pacific Northwest. American Fisheries Society Syposium 17:334-349.

Rice, S. 1994. Towards a model of changes in bed material texture at the drainage basin scale. Pages 161-172. *in* Kirkby, M.J., editor. Process models and theoretical geomorphology. Wiley.

Robinson, C.T., U. Uehlinger, and G.W. Minshall. 2005. Functional characteristics of wilderness streams twenty years following wildfire. Western North American Naturalist 65:1-10.

Robison, E.G., and R.L. Beschta. 1990. Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences 47:1684-1693.

Romme, W. H., and D.H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming Ecology 62:319-326.

Sobota, D.J. 2003. Fall directions and breakage of riparian trees along streams in the Pacific Northwest. M.S. Thesis. Oregon State University. Corvallis, Oregon.

Spies, T.A., J.F. Franklin, and T.B Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69:1689-1702.

Swanson, F. J., G.W. Lienkaemper, and J.R. Sedell. 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. General Technical Report PNW-56, USDA Forest Service.

Swanson, F. J., and G.W. Lienkaemper. 1978. Physical consequences of large organic debris in Pacific Northwest streams. General Technical Report PNW-69, USDA Forest Service.

Swanson, F. J. 1981. Fire and geomorphic process. General Technical Report WO-26, U.S. Forest Service.

Van Sickle, J., and S.V. Gregory. 1990. Modeling inputs of large woody debris to streams from falling trees. Canadian Journal of Forest Research 20:1593-1601.

Welch, D. M. 1970. Substitution of space for time in a study of slope development. Journal of Geology 78:234-238.

Wolman, M. G. 1954. A method of sampling coarse river-bed material. Eos Transactions AGU 35:951-956.

Wolman, M. G., and J. P. Miller. 1960. Magnitude and frequency of forces in geomorphic processes. Journal of Geology 68:54-74.

Wolman, M. G., and R. Gerson. 1978. Relative scales of time and effectiveness of climate in watershed geomorphology. Earth Surface Processes 3:189-208.

Wondzell, S.M., and J.G. King. 2003. Postfire erosional processes in the Pacific Northwest and rocky mountain regions. Forest Ecology and Management 6238:1-13.

Zimmerman, G. M., H. Goetz, and P.W. Mielke, Jr. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology 66:606- 611.

APPENDIX

Appendix A1. Sites classified by time since basin burn.

Basin Burn Classification		Controls					Characteristics	
Stream	Treatment	Elevation (m)	Valley width (channel widths)	Valley Slope (m/m)	Drainage Area (ha)	Average Basin Slope (m/m)	Discharge (m^3/s)	Stream Order
Cottonwood	Recent	2053	4	0.039	1178	0.33	1.85	4
E. Fk. Elk	Recent	2103	9	0.038	1175	0.28	3.82	3
Farrow	Recent	1980	5	0.033	894	0.37	2.93	3
Lodgepole (Idaho Co.)	Recent	1932	4	0.023	1180	0.43	2.07	3
No name (trib to N. Fk Elk)	Recent	1997	4	0.024	968	0.27	4.24	3
W. Fk. Chamberlain	Recent	1850	8	0.024	813	0.40	3.54	3
Bridge	Mid	1488	4	0.03	815	0.20	3.62	3
Frank Brown	Mid	1727	5	0.028	902	0.21	3.43	3
L. Mallard	Mid	1793	8	0.029	665	0.21	2.63	3
Otterson	Mid	1471	3	0.025	920	0.23	3.82	3
Porter	Mid	2076	3	0.028	709	0.25	3.60	3
Rock	Mid	2078	3	0.037	699	0.33	3.32	3
U.20 Mile	Mid	1846	4	0.029	699	0.28	3.61	3
VanBuren	Mid	1634	5	0.035	557	0.39	3.76	3
W. Fk. 20 Mile	Mid	1328	4	0.028	1106	0.15	2.06	3
4-Mile	Old	1782	6	0.034	645	0.13	3.54	3
6-Bit	Old	1852	3	0.031	911	0.35	3.40	3
Lodgepole (Valley Co.)	Old	1776	7	0.039	876	0.39	3.19	3
N. Fk. Hotsprings	Old	1557	4	0.036	686	0.33	3.12	2
No name (trib to Bargaman cr.)	Old	1549	5	0.027	658	0.29	3.02	2
S. Fk. Hotsprings	Old	1564	4	0.037	443	0.33	2.27	2
Upper Big Mallard	Old	1950	3	0.024	412	0.09	3.13	3
Winnemucca	Old	2215	4	0.028	793	0.27	3.21	3
Recent Mean		1986	5.67	0.030	1035	0.347	3.07	
Mid Mean		1716	4.33	0.030	786	0.251	3.32	
Old Mean		1781	4.50	0.032	678	0.273	3.11	
Group Mean		1809	4.74	0.031	813	0.284	3.18	

Appendix A2. Sites classified by time since riparian burn.

Riparian Burn Classification		Controls					Characteristics	
Stream	Treatment	Elevation (m)	Valley width (channel widths)	Valley Slope (m/m)	Drainage Area (ha)	Average Basin Slope (m/m)	Discharge (m^3/s)	Stream Order
E. Fk. Elk	Recent	2103	9	0.038	1175	0.28	3.82	3
Farrow	Recent	1980	5	0.033	894	0.37	2.93	3
Lodgepole (Idaho Co.)	Recent	1932	4	0.023	1180	0.43	2.07	3
No name (trib to N. Fk Elk)	Recent	1997	4	0.024	968	0.27	4.24	3
Bridge	Mid	1488	4	0.03	815	0.20	3.62	3
Frank Brown	Mid	1727	5	0.028	902	0.21	3.43	3
L. Mallard	Mid	1793	8	0.029	665	0.21	2.63	3
Otterson	Mid	1471	3	0.025	920	0.23	3.82	3
Porter	Mid	2076	3	0.028	709	0.25	3.60	3
U.20 Mile	Mid	1846	4	0.029	699	0.28	3.61	3
W. Fk. Chamberlain	Mid	1850	8	0.024	813	0.40	3.54	3
4-Mile	Old	1782	6	0.034	645	0.13	3.54	3
6-Bit	Old	1852	3	0.031	911	0.35	3.40	3
Cottonwood	Old	2053	4	0.039	1178	0.33	1.85	4
Lodgepole (Valley Co.)	Old	1776	7	0.039	876	0.39	3.19	3
N. Fk. Hotsprings	Old	1557	4	0.036	686	0.33	3.12	2
No name (trib to Bargaman cr.)	Old	1549	5	0.027	658	0.29	3.02	2
Rock	Old	2078	3	0.037	699	0.33	3.32	3
S. Fk. Hotsprings	Old	1564	4	0.037	443	0.33	2.27	2
Upper Big Mallard	Old	1950	3	0.024	412	0.09	3.13	3
VanBuren	Old	1634	5	0.035	557	0.39	3.76	3
W. Fk. 20 Mile	Old	1328	4	0.028	1106	0.15	2.06	3
Winnemucca	Old	2215	4	0.028	793	0.27	3.21	3

Recent Mean		2003	5.50	0.030	1054	0.337	3.26
Mid Mean		1750	5.00	0.028	789	0.256	3.46
Old Mean		1778	4.33	0.033	747	0.282	2.99
Group Mean		1809	4.74	0.031	813	0.284	3.18

Appendix A3. Sites classified by time since synchronous basin and riparian burn.

Synchronous Burn Classification		Controls					Characteristics	
Stream	Treatment	Elevation (m)	Valley width (channel widths)	Valley Slope (m/m)	Drainage Area (ha)	Average Basin Slope (m/m)	Discharge (m^3/s)	Stream Order
E. Fk. Elk	Recent	2103	9	0.038	1175	0.28	3.82	3
Farrow	Recent	1980	5	0.033	894	0.37	2.93	3
Lodgepole (Idaho Co.)	Recent	1932	4	0.023	1180	0.43	2.07	3
No name (trib to N. Fk Elk)	Recent	1997	4	0.024	968	0.27	4.24	3
Bridge	Mid	1488	4	0.03	815	0.20	3.62	3
Frank Brown	Mid	1727	5	0.028	902	0.21	3.43	3
L. Mallard	Mid	1793	8	0.029	665	0.21	2.63	3
Otterson	Mid	1471	3	0.025	920	0.23	3.82	3
Porter	Mid	2076	3	0.028	709	0.25	3.60	3
U.20 Mile	Mid	1846	4	0.029	699	0.28	3.61	3
4-Mile	Old	1782	6	0.034	645	0.13	3.54	3
6-Bit	Old	1852	3	0.031	911	0.35	3.40	3
Lodgepole (Valley Co.)	Old	1776	7	0.039	876	0.39	3.19	3
N. Fk. Hotsprings	Old	1557	4	0.036	686	0.33	3.12	2
S. Fk. Hotsprings	Old	1564	4	0.037	443	0.33	2.27	2
No name (trib to Bargaman cr.)	Old	1549	5	0.027	658	0.29	3.02	2
Upper Big Mallard	Old	1950	3	0.024	412	0.09	3.13	3
Winnemucca	Old	2215	4	0.028	793	0.27	3.21	3
Recent Mean		2003	5.50	0.030	1054	0.337	3.26	
Mid Mean		1734	4.50	0.028	785	0.232	3.45	
Old Mean		1781	4.50	0.032	678	0.273	3.11	
Group Mean		1814	4.72	0.030	797	0.273	3.26	

Appendix A4. Pool and riffle-crest substrate classifications:

1. Wood (used only for riffle crest depth)
2. Sand, < 2mm
3. Fine gravel, 2-8 mm
4. Coarse, gravel >8-64 mm
5. Cobble, >64-256 mm
6. Boulder, >256 mm

Appendix A5. Wood decay classifications stratified by submergence and burn combinations:

	Decay Class			
Wood Type	1 (young)	2	3	4 (old)
Submerged (not burned)	Needles present on any part of tree (including outside of the channel/submerged volume)	No bark and the surface is smooth, or bark and no branches	Bole surface rough and soft	Gnarled bole and very hard (generally black)
Not submerged (not burned)	Needles present on any part of the tree	Some loose bark, but most is firmly attached, or no bark and bole is smooth	Bark is easily pulled off bole, wood losing integrity	Very soft, crumbly
Submerged (burned)	Burnt bark and limbs, or no bark and limbs due to fire	Bole is smooth	Bole surface rough and soft	Gnarled bole and very hard (generally black)
Not submerged (burned)	Burnt bark and limbs, or no bark and limbs due to fire	No bark, some surface cracks, wood sound	Extensive cracks, wood losing integrity	Very soft, crumbly

Appendix A6. Site characteristics.

Stream	Average residual pool depth (m)	Average pool spacing (acw)*	Average cross section area (m^2)*	Average hydraulic radius (m^2/m)*	Average active channel width (m)	Average active channel depth (m)	Average bank-full depth (m)	Sinuosity	Valley Slope (m/m)	Wood amount (pieces/100 m)
Cottonwood	0.15	10.71	0.87	0.26	2.50	0.15	0.28	1.12	0.039	23.44
E. Fk. Elk	0.3067	2.47	2.48	0.44	4.45	0.28	0.51	1.37	0.038	90.80
Farrow	0.2956	5.01	1.48	0.35	2.88	0.22	0.33	1.25	0.033	78.70
Lodgepole (Idaho Co.)	0.3189	3.80	1.30	0.39	2.29	0.24	0.43	1.51	0.023	74.01
No name (trib to N. Fk Elk)	0.2867	7.31	2.50	0.48	3.55	0.24	0.54	1.20	0.024	94.84
W. Fk. Chamberlain	0.2056	4.80	1.69	0.39	2.97	0.19	0.40	1.27	0.024	45.63
Bridge	0.2011	3.20	2.04	0.37	3.47	0.27	0.46	1.43	0.03	69.80
Frank Brown	0.2922	3.87	1.51	0.32	3.53	0.22	0.36	1.21	0.028	46.00
L. Mallard	0.3589	2.96	1.67	0.40	3.12	0.30	0.42	1.42	0.029	89.29
Otterson	0.2711	3.71	1.99	0.42	3.10	0.24	0.45	1.25	0.025	75.45
Porter	0.4011	8.61	2.22	0.41	4.20	0.22	0.43	1.20	0.028	36.92
Rock	0.3367	6.90	1.64	0.39	2.90	0.26	0.43	1.15	0.037	73.00
U.20 Mile	0.2456	3.66	2.22	0.42	4.21	0.28	0.44	1.89	0.029	58.75
VanBuren	0.2125	3.53	2.10	0.37	4.02	0.30	0.44	1.11	0.035	61.73
W. Fk. 20 Mile	0.2333	4.83	1.30	0.32	3.02	0.20	0.36	1.16	0.028	84.48
4-Mile	0.2511	7.01	2.10	0.35	4.78	0.19	0.33	1.08	0.034	81.48
6-Bit	0.4167	6.23	2.50	0.44	4.10	0.29	0.46	1.11	0.031	119.03
Lodgepole (Valley Co.)	0.3056	9.09	2.19	0.36	4.55	0.24	0.36	1.22	0.039	71.66
N. Fk. Hotsprings	0.2778	1.85	2.15	0.36	4.73	0.31	0.41	1.23	0.036	81.11
No name (trib to Bargaman cr.)	0.3311	3.12	1.70	0.35	3.20	0.23	0.37	1.28	0.027	73.75
S. Fk. Hotsprings	0.2122	3.43	1.21	0.33	2.57	0.32	0.39	1.18	0.037	81.25
Upper Big Mallard	0.3211	5.19	2.10	0.40	3.75	0.37	0.45	1.68	0.024	69.31
Winnemucca	0.2	12.39	1.75	0.37	3.36	0.17	0.40	1.23	0.028	41.15

Appendix A7. Percent of stand burned in the basin versus within the riparian zone. Percent burn values correspond with times of fire, respectively. For old stands, it was not possible to determine the percent of the basin burned with aerial photography, nor was it possible to use stand cruise data to determine the percent of the riparian stand that burned, due to the extensive time since fire. Hence, old basin and riparian stands were ones where less than 50 percent of the forest had burned within 150 years of the study.

	Basin burn treatments	Time of fire(s)	% basin burned	% riparian burned
Cottonwood	Recent	1988	75	20
E. Fk. Elk	Recent	1987	70	66
Farrow	Recent	1987	95	60
Lodgepole (Idaho Co.)	Recent	1986, 2000	90, 10	60, 0
No name (trib to N. Fk Elk)	Recent	1987	70	47
W. Fk. Chamberlain	Recent	1966, 2000	75,25	10, 0
Bridge	Mid	1919	50	36
Frank Brown	Mid	1919	70	55
L. Mallard	Mid	1870, 1910	30, 60	0,42
Otterson	Mid	1919	80	98
Porter	Mid	1910	80	64
Rock	Mid	1900	70	0
U.20 Mile	Mid	1919	85	52
VanBuren	Mid	1910	60	0
W. Fk. 20 Mile	Mid	1919	75	0
4-Mile	Old	1773, 1910	?, 35	?, 0
6-Bit	Old	1843, 1910	?, 30	?, 0
Lodgepole (Valley Co.)	Old	1773, 1910	?, 20	?, 0
N. Fk. Hotsprings	Old	1833, 1910	?, 30	?, 18
No name (trib to Bargaman cr.)	Old	1833, 1911	?, 30	?, 0
S. Fk. Hotsprings	Old	1803, 1910	?, 40	?, 31
Upper Big Mallard	Old	1853, 1919	?, 35	?, 0
Winnemucca	Old	1843, 1910	?, 30	?, 0

RESEARCH AREA 3: EFFECTS OF WILDFIRE AND ECOLOGICAL CONTEXT ON AQUATIC BIOLOGICAL DIVERSITY

Postdoctoral research of
Amanda E. Rosenberger

OVERVIEW

The Rocky Mountain Research Station initiated a multi-year study on the effects of wildfire and ecological context on aquatic biological diversity. Products from this work provide assistance to management by providing new tools for monitoring stream-living aquatic vertebrate responses to fire, predicting the effects of wildfire on nonnative species invasions, and predicting the effects of wildfire on native species and assemblages. This report provides details results related to specific goals outlined in our workplan, which form the bases for the following sections under Research Area 3:

1. Develop new tools for monitoring aquatic vertebrate population responses to fire.
2. Understand responses of key habitat variables to fire (channel structure, dynamics, and stream temperature) and better understand key environmental gradients and how they are distributed across the landscape.
3. Develop models to:
  a. Predict responses of native aquatic vertebrates to fire and related influences
  b. Construct hypotheses about cause-and-effect relationships between aquatic vertebrates, fire, and related influences
4. Work with managers to develop applications of these results in prioritization of fire management alternatives to benefit native aquatic vertebrates and to deal effectively with nonnative fish invasions.

Accomplishments

Goal 1: We developed a validated approach for measuring rainbow trout abundance in small headwater streams and published our results in a peer-reviewed manuscript for the *North American Journal of Fisheries Management.* We also validated an approach for measuring fish maturity and the sex of mature fish non-lethally using endoscopy. These results were published in *Transactions of the American Fisheries Society.*

Goal 2: We have quantitatively examined the effects of wildfire and channel reorganization on spatial and temporal variation in stream temperature and directly related that variability to the distribution of fish an amphibians in the Boise River Basin. The results of this work have been published in the journal *Ecosystems.* In addition, we prepared a manuscript on the effects of wildfire and channel reorganization on drifting macroinvertebrates and predation by trout in headwater streams of the Boise River Basin to be submitted to *Transactions of the American Fisheries Society.* Finally, we completed an unpublished analysis of the effects of wildfire and channel-reorganizing events on channel morphology.

Goal 3: Using an integrated approach of field data and individual-based model simulations, we have investigated population and individual responses of rainbow trout, the most widely distributed fish in headwater streams of the basin, to wildfire and channel disturbance. Although this analysis has been completed and is reported here, the final manuscript is still in preparation and will be submitted to *Ecological Applications.*

Goal 4: We have disseminated our results widely and had frequent interactions with managers and policy makers regarding the effects of wildfire and channel disturbance on aquatic ecosystems.

In this final report, we include all details for these studies in manuscript form separated by the goals outlined in the original workplan. For readers who do not wish to comprehensively read all of the details of published studies, we include abstracts for faster review.

GOAL 1: DEVELOP NEW TOOLS FOR MONITORING AQUATIC VERTEBRATE POPULATION RESPONSES TO FIRE

We have published two manuscripts related to this goal:

1. Rosenberger, A.E. and J.B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. *North American Journal of Fisheries Management* 25:1395–1410.
2. Swenson, E.A., A.E. Rosenberger, and P.J. Howell. 2007. Validation of endoscopy for non-lethal determination of maturity of small brook trout. *Transactions of the American Fisheries Society* 136:994-998.

The following sections contain the content of the two manuscripts.

RESEARCH AREA 3 * GOAL 1 * PUBLICATION I

Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams

Abtract.— Estimation of fish abundance in streams using removal or Lincoln-Peterson mark-recapture models is a common practice in fisheries. These models produce misleading results if their assumptions are violated. We evaluated the assumptions of these two models via electrofishing of rainbow trout *Oncorhynchus mykiss* in central Idaho streams. For 1-, 2-, 3-, and 4-pass sampling effort in closed sites, we evaluated the influences of fish size and habitat characteristics on sampling efficiency and the accuracy of removal abundance estimates. We also examined the use of models to generate unbiased estimates of fish abundance through adjustment of total catch or biased removal estimates. Our results suggested that assumptions of the mark-recapture model were satisfied and abundance estimates using this approach were unbiased. In contrast, removal model assumptions were not met. Decreased sampling efficiency over removal passes resulted in underestimated population sizes and overestimated sampling efficiency. This bias decreased, but was not eliminated, with increased sampling effort. Biased removal estimates based on different levels of effort were highly correlated, but less correlated with unbiased mark-recapture estimates. Stream size decreased sampling efficiency, and stream size and instream wood increased negative bias of removal estimates. We found that reliable estimates of population abundance could be obtained from models of sampling efficiency for different levels of effort. Validation of abundance estimates requires extra attention to routine sampling considerations, but also can help fisheries biologists avoid pitfalls associated with biased data and facilitate standardized comparisons among studies using different sampling methods.

Introduction

Estimation of fish population sizes is a fundamental activity for fisheries management and research. The validity of abundance estimates is a function of how well and how consistently they approximate actual fish numbers. Abundance estimates for stream fish often rely on active capture of fish by nets, toxicants, or electrofishing (Murphy and Willis 1996), and it is widely known that no method is 100% effective. Therefore, assessment of fish abundance begins with an assessment of the proportion of the total number of fish present that are captured in a sample, or sampling efficiency. Sampling efficiency for a variety of methods can be affected by habitat complexity (Rodgers et al. 1992; Kruse et al. 1998; Mullner et al. 1998), habitat size (Bayley and Dowling 1993; Kruse et al. 1998; Peterson et al. 2004), fish species and size (Büttiker 1992; Bayley and Dowling 1993; Dolan and Miranda 2003), density of fishes (Simpson 1978; Kruse et al. 1998), and level of effort (Riley and Fausch 1992; Riley et al. 1993; Peterson et al. 2004).

Abundance estimates from electrofishing capture data are most often generated using removal or mark-recapture models (Otis et al. 1978; White et al. 1982; Thompson et al. 1998). The removal model uses catch data from depletion sampling to estimate sampling efficiency and population size. Depletion sampling is accomplished in most cases with one site visit, and removal estimates are obtained using available software (e.g., Otis et al. 1978; White et al. 1982). Removal model assumptions are a closed population and equal capture probability for all individuals and all sampling occasions (e.g., depletions, electrofishing passes). Use of effective movement barriers during sampling can satisfy the first assumption, but the second assumption is more difficult to address. Although the time spent actively sampling or the area sampled can be held constant over successive capture occasions, fish that remain after initial passes may be less catchable, resulting in lower sampling efficiency from pass to pass. For example, larger fish are easier to capture than smaller fish (Büttiker 1992; Bayley and Dowling 1993; Dolan and Miranda 2003; Peterson et al. 2004). Also, fish that remain after initial capture occasions may be less catchable due to physiological or behavioral response to the disturbance of the previous passes (Mesa and Schreck 1989). The removal model overestimates sampling efficiency and underestimates population size under conditions of decreasing sampling efficiencies (Zippin 1958; Riley and Fausch 1992). This can be addressed with a generalized removal estimator that adjusts for differences among passes in sampling efficiency; however, this approach requires at least four capture occasions and detection of heterogeneity using a goodness-of-fit test (Otis et al. 1978).

The Lincoln-Peterson mark-recapture model is a widely used alternative to the removal model (Thompson et al. 1998). This approach is computationally simple, but more field-intensive than the removal method. Mark-recapture estimator assumptions are a closed population, random distribution of marked and unmarked individuals, and no difference in capture probability between marked and unmarked fish (White et al. 1982). As with the removal method, the closure assumption can be addressed through adequate use of movement barriers. The remaining assumptions can be addressed by allowing a sufficient recovery period between marking and recapture (e.g., 24 h; Mesa and Schreck 1989; Peterson et al. 2004). Presumably because it is easier to meet these assumptions for stream fish, mark-recapture abundance estimates appeared less biased when compared to removal estimates (Rodgers et al. 1992).

Unbiased abundance estimates are difficult and time-consuming to obtain. This can limit the spatial extent of scientific or management endeavors and decrease understanding of large-scale patterns of fish abundance (Hankin and Reeves 1988). This problem has led to attempts to obtain unbiased abundance estimates by comparing numbers from a low intensity but biased method of sampling fish (e.g., snorkeling or single pass counts) to more intensive and model-based population estimates that are assumed to be unbiased (e.g., multiple pass removal estimates). If low intensity numbers and high intensity estimates are strongly correlated, these studies typically conclude that low intensity numbers can be calibrated or used as a relative measure of abundance (Hankin and Reeves 1988; Simonson and Lyons 1995; Lobón-Cerviá and Utrilla 1993; Thurow and Schill 1996; Kruse et al. 1998; Mullner et al. 1998; Joyce and Hubert 2003). Though intuitively and practically appealing, this validation method (an "index-to-index" comparison) is problematic. Factors such as habitat features can contribute to bias in both low and high intensity numbers (Thompson 2003), and the relationship between the two indices may vary unpredictably in different contexts (Williams et al. 2004). Validation of abundance estimates instead requires a comparison of the estimate against an unbiased account of fish abundance (an "index to unbiased estimate" comparison). Unbiased numbers can be obtained via release of a known number of marked individuals into a site (Rodgers et al. 1992; Peterson et al. 2004) and/or using a model whose assumptions can be rigorously tested or addressed.

In this study, we describe electrofishing sampling efficiency for rainbow trout *Oncorhynchus mykiss* in small mountain streams. Our objectives were to assess the accuracy of modeled abundance estimates and evaluate multiple calibration approaches that adjust catch data or removal estimates to reflect valid measures of abundance. We: 1) determined site-scale correlates of sampling efficiency; 2) tested mark-recapture and removal model assumptions; 3) compared 2-, 3-, and 4-pass removal estimates with less biased measures of fish abundance; 4) examined correlates of removal estimate bias; and 5) examined the feasibility of calibrating removal catch data to reflect valid measures of fish abundance using predictions from sampling efficiency models and models of removal estimate bias. For calibration models, we considered cumulative catch data from 1-, 2-, 3-, or 4 passes to determine if and how much increasing sampling effort (measured as the number of passes completed) improved model predictions. We discuss our results in light of developing validation protocols that can produce standardized estimates of fish abundance.

Methods

Study Area.—We conducted our study in the Salmon-Challis and Boise National Forests in central and southwestern Idaho. Study sites were located in small, headwater tributaries of the Middle, North, and South forks of the Boise River and Panther Creek, a tributary of the Salmon River. This study is part of an ongoing project examining the effects of wildfire on aquatic systems, and streams were selected to represent the range of characteristics that we expect to encounter for the duration of this larger project (Table 3.1.I 1). Sites within those streams were selected based on accessibility. We sampled during July-September 2002 and 2003 at or near baseflow conditions.

Field Methods.—Each site was approximately 100 m in length (Table 3.1.I 1). Prior to sampling, crews blocked off the upstream and downstream ends of the site with 7 mm mesh nets secured to

the streambed at habitat unit breaks. To evaluate potential bias from escapement (violation of the closed-population assumption), we equipped a subset of our sites with double block nets at both ends (n = 11 sites; following Peterson et al. 2004). After block nets were in place, we conducted a single electrofishing pass using a Smith-Root backpack electrofisher (LR-24 or 12B Electrofisher, Vancouver, WA) with pulsed direct current (DC). Crews adjusted voltage, pulse, and frequency to maximize capture probability without causing fish injury (settings range: voltage = 400-700, frequency = 30-50 Hz, pulse width = 2-8 ms). Rainbow trout from the initial marking pass were anaesthetized with MS-222, measured for fork length to the nearest mm, and, if greater than 60 mm in length, marked by taking a fin clip from the dorsal tip of the caudal fin. Live wells with ambient stream water held all captured fish during processing. Crews returned marked individuals throughout the length of the closed site to encourage random dispersal. Fish that did not appear healthy were released below the site and were not included in the marked fish population. This marked population served as an unbiased baseline abundance estimate (Riley et al. 1993; Peterson et al. 2004).

After the marking pass and at least one overnight recovery period, crews carried out 4-pass depletion sampling within the closed site. To assist in evaluation of potential bias from changes in fish behavior after marking and handling (violation of the equal capture probability assumption of the mark-recapture model), crews varied the time between marking and the first removal (recapture) pass (hereafter, recovery period; range = 15.4 – 47.3 h). Following completion of each removal, fish were identified, checked for marks, and measured for fork length to the nearest mm. If double block nets were present, crews sampled between nets to detect marked fish that escaped from the original site. All block nets remained in position for the duration of removal sampling. Live wells held all captured fish at stream margins outside of the site until all 4 passes were completed. Times between removal passes were variable and did not include an explicit "resting period" to allow fish to recover from previous electrofishing activity. All available habitats within the site were sampled. We could have implemented a more strict protocol to "standardize" sampling effort (e.g., shocking time, time between passes, shocker settings), but our point was to emulate common practice for fishery biologists in the region. We reasoned this approach would provide the most useful and generally applicable information.

For each site, we recorded its length (m), slope (%, measured with a stadia rod and hand level), elevation (m), maximum depth (cm), and mean temperature (°C) from measurements taken at the beginning and end of each pass. We also counted instream wood (> 10cm in diameter and > 1 m in length) and aggregates (> 4 pieces of wood acting as a single component). In addition, crews placed transect lines perpendicular to the channel over the length of the site, with a spacing of 5 m. For each transect, crews measured wetted channel width (m), mean depth (cm; Overton et al. 1997), and, at 7 points, dominant substrate characteristics within a 10 cm diameter circle. Substrate categories were defined using an Udden-Wentworth grain-size scale following Buffington and Montgomery (1999): 1 = Silt <1/16 mm; 2 = Sand 1/16-2 mm; 3 = Gravel 2-64 mm; 4 = Cobble >64-256 mm; 5 = Boulder >256 mm; 6 = Bedrock. Larger particles were "embedded" if predominantly surrounded by silt or sand. Total length of undercut banks >10 cm in depth, height and length were recorded if they intersected horizontal transects.

Data Analysis

Objective 1-Evaluation of site-scale correlates of sampling efficiency.— With logistic regression, we modeled overall (cumulative, 4-pass) sampling efficiency based on site-scale habitat and fish population characteristics using SAS (SAS® Version 9.1, Cary, NC[1]). Mean cross-sectional area, total length of undercut banks, and total wet debris were Log_{10} transformed to meet normality assumptions. Pearson correlations were run on all pairs of predictor variables prior to modeling to test for collinearity (maximum r observed = 0.53). We estimated overall sampling efficiency in two ways: 1) cumulative 4-pass catch of marked fish divided by number of marked fish released into the site and 2) cumulative 4-pass catch of fish > 60 mm (marked and unmarked) divided by the mark-recapture abundance estimate of fish > 60 mm. We used the Lincoln-Peterson mark-recapture model, as modified by Chapman (1951). Cumulative 4-pass catch of marked fish served as the number of recaptures for mark-recapture estimates. When we used the known number of marked fish released our baseline measure of fish abundance, we could directly measure sampling efficiency using the number of recaptures; therefore, we described marked fish sampling efficiency as "measured sampling efficiency," following Peterson et al. (2004). We use the term, "mark-recapture sampling efficiency" for estimated sampling efficiency based on mark-recapture estimates divided by the total number of fish > 60 mm captured.

We used an information-theoretic approach (Burnham and Anderson 2002) for hypothesis testing and model selection. We began by constructing a global model using information from previous studies to select site-scale features (Table 3.1.I 1) most likely to influence sampling efficiency. Candidate models were subsets of the global model based on frequently cited combinations of variables that affect electrofishing sampling efficiency. We categorized these variables into four groups: stream size, cover, mean stream temperature, and fish size. We used mean cross-sectional area (the product of mean stream depth and width) as our measure of stream size (Peterson et al. 2004). Cover included total length of undercut banks, total count of instream wood, and percent cobble. Median fork length of captured fish > 60 mm was used as an overall measure of fish size. We anticipated that stream size and cover would reduce sampling efficiency, whereas an increase in stream temperature and median fish length would improve sampling efficiency. After testing the significance of the global model and model assumptions, we selected the most likely model using Akaike's Information Criteria (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Burnham and Anderson 2002). The relative plausibility of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002). If model selection did not indicate overwhelming evidence for a single candidate model, we averaged predictor variables across all candidate models whose Akaike weights were more than one-eighth of the largest weight to form an averaged composite model (recommended by Royall 1997). We used a weighted mean based on Akaike weights to calculate averaged model parameter estimates (Burnham and Anderson 2002).

Objective 2-Evaluation of mark-recapture and removal model assumptions.— To evaluate the closed-population assumption of the mark-recapture model, we compared mark-recapture estimates with and without 'escapees' (marked fish found outside of the site between double block nets). We corrected mark-recapture estimates for escapement in all subsequent analyses.

Electrofishing can alter fish behavior for up to 24 hours (Mesa and Schreck 1989), which could be exacerbated by handling and fin clip removal. An inadequate recovery period would result in an unequal capture probability between marked and unmarked fish, violating a mark-recapture model assumption. We used logistic regression to examine the relationship between recovery period (recovery period range = 15.4 to 47.3 hr, mean = 23.2 ± 6.8, SD) and measured sampling efficiency. No relationship would signify that marking had a negligible effect on sampling efficiency and was not a significant source of mark-recapture estimate bias.

The removal estimator obtained from the program CAPTURE (White et al. 1982) was used to estimate abundance of marked rainbow trout and all rainbow trout > 60 mm within sites (White et al. 1982). We obtained separate removal estimates of fish abundance using 2, 3, or all 4 passes. For 4-pass removal estimates only, we used the generalized removal model that can account for heterogeneity in sampling efficiency among passes detected using a goodness-of-fit test (Otis et al. 1978; White et al. 1982). We were able to use the generalized removal model to estimate total abundance of fish > 60 mm in the site; sample sizes of marked fish were too small (n individuals marked range: 2-60, mean = 17 ± 13, SD; n marked individuals recovered: range = 2-43, mean = 12 ± 9, SD). In all other cases, we used the Zippin removal estimator, which assumes equal capture probability among removal passes.

Violation of the constant-capture probability assumption is the most likely source of bias in removal estimates (White et al. 1982). Therefore, for each electrofishing depletion pass, we compared estimated sampling efficiencies based on the removal model (henceforth, removal model sampling efficiency) with measured sampling efficiencies. We also examined if measured sampling efficiency was heterogeneous over all 4 successive passes using a log-likelihood G-test (alpha values adjusted for multiple tests using the Dunn-Sidak correction; adjusted $\alpha = 0.001$; Sokal and Rohlf 1995). Results from these direct tests on measured sampling efficiencies were compared in a case-by-case manner to results from the generalized model goodness-of-fit tests on 4-pass removal data of all fish > 60 mm (Zippin 1958; Otis et al. 1978; White et al. 1982). The comparison served as an assessment of how well the goodness-of-fit test detected sizeable heterogeneity when present.

Objective 3-Evaluation of removal estimate bias.— We measured removal estimate bias in two ways: 1) comparison of marked fish removal estimates to known number of marked fish returned to the closed site and 2) comparison of removal estimates of all fish > 60 mm to mark-recapture estimates of all fish > 60 mm. The first comparison was a more exact assessment of estimate bias but limited in terms of the range of fish abundance (see above). The second comparison had potential for inaccuracy but better emulated the range of fish densities typical of our study area (12-155 individuals captured per 100 m site). To examine the effect of effort on bias, we made these comparisons separately for 2-, 3-, and 4- pass removal estimates.

Objective 4: Site-scale correlates of removal estimate bias.—We used linear regression to examine the relationship between 4-pass removal estimate bias and site characteristics. We expressed and modeled bias of removal estimates in two ways: 1) marked fish removal estimates/ known number of marked fish returned to the closed site; 2) removal estimates of all fish > 60 mm/ mark-recapture estimate of all fish > 60 mm. Because factors influencing sampling efficiency can similarly affect removal estimate bias (Peterson et al. 2004), we considered the

same habitat variables that were included in sampling efficiency models. For model selection, averaging, and inference, we used the Burnham and Anderson (2002) information-theoretic approach described previously. We examined equality of variances through visual examination of residuals, Levene's test of homogeneity of variances on absolute residual deviations, and correlations between absolute residual deviations and model variables.

Objective 5: Model prediction of fish abundance.—We evaluated three approaches for unbiased prediction (calibration) of fish abundance: 1) models of sampling efficiency, 2) direct calibration of catch without consideration of site-scale correlates of sampling efficiency; and 3) calibration of removal estimates via models of removal estimate bias, with and without habitat covariates. For simplicity and to avoid falsely inflating measures of predictive power, calibration models with site-scale covariates included only those covariates that influenced sampling efficiency in previous analyses (Objectives 1 and 4). In all cases, mark-recapture estimates were used as baseline measures of fish abundance. Although these estimates are more subject to error than known numbers of marked fish released, they better reflect the typical range of abundances in our study area.

Calibration from sampling efficiency.— We used logistic regression models predicting cumulative mark-recapture sampling efficiency after 1, 2, 3, and 4 passes. To have a measure of how well our regression models predicted new observations, we used leave-one-out-cross validation for predictions of sampling efficiency for each occasion. These modeled estimates of sampling efficiency against known catch were used to predict fish abundance (predicted fish abundance = known catch /predicted sampling efficiency). These predictions were plotted against mark-recapture estimates and the strength of that relationship (R^2) indicated the predictive power of the sampling efficiency model under a leave-one-out scenario.

Direct calibration of catches. —We also used linear regression to predict mark-recapture abundance estimates based on fish catches alone. We used a similar leave-one-out validation approach via calculation of Prediction Sum of Squares (PRESS) residuals (Myers 1990). PRESS residuals are estimated by withholding a single observation (y_i) and calculating a y_i residual by subtracting the observed value from that predicted by a regression model constructed with the remaining observations (n-1). We compared PRESS residuals with residuals estimated from the overall means model with an R^2-like statistic (R^2_{Pred}) that indicates the overall predictive performance (Myers 1990). We examined equality of variances through visual examination of residuals, the Levene's test of homogeneity of variances on absolute residual deviations, and correlations between absolute residual deviations and model variables.

Calibration of biased removal estimates.— To examine if 2-, 3-, or 4-pass removal estimates were good predictors of unbiased measures of fish abundance, we used linear regression models of removal estimate bias with and without site-scale covariates. PRESS residuals were used to calculate R^2_{Pred} as described above to assess the predictive abilities of these models. Model assumptions were tested as described above.

Results

Objective 1- Evaluation of site-scale correlates of sampling efficiency.—We constructed two logistic regression models, one modeling measured sampling efficiency (cumulative number of marked fish recaptured over 4 passes/ number of marked fish released into the site), the other modeling mark-recapture sampling efficiency (cumulative catch of fish > 60 mm over 4 passes/ mark-recapture estimate of fish > 60 mm). The most likely model of measured sampling efficiency included only mean cross-sectional area, our measure of stream size (Table 3.1.I 2). Confidence intervals around the mean cross-sectional area parameter estimate and the model intercept did not overlap zero. The most likely model for mark-recapture sampling efficiency included stream size, mean temperature, and median fish length; however, in all cases, confidence intervals overlapped zero, indicating unpredictable effects on mark-recapture sampling efficiency (Table 3.1.I 2). Strong evidence for both models (high AIC weights) precluded model averaging.

Objective 2-Evaluation of mark-recapture and removal model assumptions.— Our measure of escapement was probably negatively biased due to two unknowns: 1) any fish that escaped from one block net may have escaped from both; and 2) it is almost certain that we did not capture 100% of fish between block nets. Escapement from sites that was detected did not present a substantial source of bias. Although escapement was observed in 5 out of the 11 sites for which double block nets were set, no more than 1 fish escape was detected per site, representing only 3% of the 164 marked trout in those sites. Correcting for escapement did not greatly change mark-recapture estimates (corrected estimate/uncorrected estimate mean = 0.95, SD = 0.05).

We found no evidence to suggest that the second assumption of equal capture probability of marked and unmarked individuals was violated over the range of recovery periods in our study. Logistic regression indicated that differences in recovery period ranging between 15.4 – 47.3 h did not affect measured sampling efficiency (Recovery period parameter estimate = 0.007, 95% CI range = -0.04 to 0.06). Further, measured sampling efficiency and recovery period were not correlated.

The removal model generally overestimated sampling efficiency (Figure 3.1.I 1). For the first pass, measured sampling efficiency exceeded removal model sampling efficiency for only 1 of 35 sites. In addition, measured sampling efficiency successively declined over removal passes (Figure 3.1.I 1). Chi-square goodness-of-fit tests of the generalized removal model performed by the program CAPTURE for each site (White et al. 1982) indicated that, with only four exceptions, capture efficiency was constant and the removal model appropriate. In contrast, log-likelihood *G*-tests performed on measured sampling efficiencies indicated that, for 17 of the 35 sites sampled, capture probabilities were heterogeneous, and removal model assumptions were not met ($G \geq 16.42$, $df \leq 2$, $P < 0.001$). Thus, in 13 out of these 17 occasions, the generalized removal model failed to detect and adjust for sizeable changes in sampling efficiency over successive passes.

Objective 3-Evaluation of removal estimate bias.—Of the 36 sites for which we obtained 4-pass marked fish removal estimates, we could calculate 3- and 2-pass estimates for only 27 and 26 of the sites, respectively. The reason for model failure was an increase in marked fish catch from

one pass to the next, indicating low and inconsistent sampling efficiency over successive passes. Regardless of how many passes were included in the model, removal estimates of marked rainbow trout were negatively biased (Figure 3.1.I 2). Bias decreased as effort increased (marked fish removal estimates/ known number of marked fish released: 2-pass mean = 0.63 ± 0.22, SD; 3-pass mean = 0.67 ± 0.26, SD; 4-pass mean = 0.75 ± 0.21, SD). Confidence intervals around 4-, 3-, and 2-pass marked fish removal estimates encompassed the number of marked fish released for only 37%, 22.5%, and 26.7% of the sites, respectively (Figure 3.1.I 2). Confidence intervals around 3-pass removal estimates were the most narrow (CV of confidence interval: 2-pass = 1.7, 3-pass = 1.1, 4-pass = 1.6).

We compared removal estimates of rainbow trout > 60 mm with mark-recapture estimates for 38 sites. Removal estimates tended to be lower than mark-recapture estimates, except for very low numbers of rainbow trout (Figure 3.1.I 3). If we eliminated occasions when the mark-recapture estimate was < 10 individuals, we saw a similar pattern of negative bias as described above. Again, bias reduced with increased sampling effort (removal estimates/ mark-recapture estimates: 2–pass mean = 0.62 ± 0.31; 3–pass mean = 0.71 ± 0.25; 4-pass mean = 0.77 ± 0.19, SD; Figure 3.1.I 3). Confidence intervals around 4-, 3-, and 2-pass removal estimates only occasionally encompassed mark-recapture estimates (30%, 31%, and 36%, respectively; Figure 3.1.I 3). Confidence intervals were again most narrow for 3-pass removal estimates (CV of confidence intervals: 4-pass = 1.5, 3-pass = 0.98, 2-pass = 2.0).

Results suggested that mark-recapture estimates were unbiased, with the exception of estimates of < 10 individuals. Low escapement and no evidence of unequal capture probability among marked and unmarked individuals indicated model assumptions were effectively addressed. Further, the pattern of removal estimate bias was the same whether marked fish released or mark-recapture estimates > 10 were used as baseline measures of abundance. For bias and calibration models described later, we used mark-recapture abundance estimates as baseline measures of fish abundance. We were less certain of mark-recapture estimates than the number of marked fish remaining in a site; however these calibration models are more widely applicable because mark-recapture estimates better reflect the range of abundances typical of our study area.

Objective 4: Site-scale correlates of removal estimate bias.— The averaged model of 4-pass marked fish removal estimate bias indicated that mean cross-sectional area contributed to negative bias (Table 3.1.I 3). All other parameters, with the exception of the model intercept, had confidence intervals that overlapped zero, indicating an inconsistent or negligible effect on bias. In the averaged model of 4-pass removal estimate bias using mark-recapture estimates as baseline measures of fish abundance, we saw a similar pattern of a positive intercept and increased negative bias with an increase in cross-sectional area. In addition, instream wood was positively related to estimate bias in this model. All other variables included in the averaged model had confidence intervals around parameter estimates that overlapped zero (Table 3.1.I 3).

Objective 5: Model prediction of fish abundance.— Models in the previous section indicated that only mean cross-sectional area and instream wood appreciably affected overall sampling efficiency or removal estimate bias. Therefore, logistic models intended for calibration purposes included only those two site-scale covariates (Table 3.1.I 4). Using mark-recapture estimates as baseline measures of fish abundance, we used a leave-one-out approach to predict sampling

efficiencies for each level of effort; these sampling efficiencies were used to generate predicted fish abundances (Table 3.1.I 4; Figure 3.1.I 4). When plotted against validated mark-recapture estimates, predicted fish abundances strongly correlated with mark-recapture estimates, regardless of sampling effort. With increased effort taken into account, the amount of variation explained by models increased, prediction intervals decreased, and slope and intercept values were closest to 1 and 0, respectively (Figure 3.1.I 4). Direct linear calibration of total catch to unbiased mark-recapture estimates without consideration of site-scale covariates of sampling efficiency resulted in much poorer calibration, particularly for low levels of effort (Table 3.1.I 5).

In general, removal estimates generated at different levels of electrofishing effort were more correlated with each other than they were with less biased mark-recapture estimates, suggesting that calibrating low effort removal indices to reflect high effort removal indices not only retains bias, but leads to false confidence of estimate precision (Table 3.1.I 6). Regardless of whether habitat variables were included in calibration models, 2- and 3-pass removal estimates were poor predictors of mark-recapture estimates compared to 4-pass removal estimates (Table 3.1.I 7), and none of the models equaled the logistic-regression models in prediction performance.

Discussion

Our results indicated that abundance estimates generated by the removal model were negatively biased and influenced by local habitat features. In contrast, we found that trout abundances could be rigorously assessed with the mark-recapture model, so long as sufficient numbers of fish were recaptured. With information on sampling efficiency and accurate abundance baselines using the mark-recapture model, we were able to develop calibrated estimates of abundance from fish catches or biased removal estimates. Strong predictive models ($R^2 > 0.80$) including site-scale covariates produced unbiased abundance estimates with relatively low effort (e.g., a single electrofishing pass); however, model predictions improved with increased sampling effort (e.g., number of removals).

Sampling efficiency and site-scale correlates of efficiency.— Our sampling approach yielded low sampling efficiencies (mean measured sampling efficiency, first pass = 44%) that decreased with successive removal passes. Stream size had a consistent negative effect on sampling efficiency, but the importance of this feature depended on whether known numbers of marked fish released in the a site (strong negative effect) or mark-recapture estimates were used as baseline measures of abundance (negative effect, but confidence intervals of the parameter estimate overlapped zero). This difference may reflect the larger range of abundances entered into the mark-recapture sampling efficiency model and/or increased potential for error in mark-recapture estimates. This underscores the importance of adhering to the common sense of avoiding model extrapolation beyond the range of data used to create the model; users should not hazard to apply models in situations for which they were not developed.

Evaluation of model assumptions and removal estimate bias.— Multiple lines of evidence suggest that our mark-recapture estimates were reliable measures of fish abundance. Presumably, this is because it was feasible to adhere to model assumptions (i.e., closed population and equal capture probability between marked and unmarked individuals). Observed escapement had a negligible effect on mark-recapture estimates. Peterson et al. (2004) reported

similarly low escapement (< 1 marked fish per 24 h), which was positively correlated with recovery period. An overnight resting period was sufficient to generate no detectable relationship between recovery time and marked fish sampling efficiency. This indicated that marked individuals had recovered sufficiently within the range of recovery periods (15.4 to 47.3h) to have the same likelihood of capture as unmarked individuals. In addition, patterns of removal estimate bias were the same whether known number of marked fish released or mark-recapture estimates were used as baseline measures of fish abundance. The exception to this was for sites with very low abundances (< 10 fish), when mark-recapture estimates appeared positively biased. This is not unexpected; Otis et al. (1978) and White et al. (1982) cautioned that mark-recapture estimates are unreliable when sampling efficiency, population size, and the number of recaptures are low.

As noted in other work, the removal model appears to be a misleading and biased method for assessing stream fish abundance. We observed negative and habitat-mediated bias of removal estimates. Low and decreasing sampling efficiency from pass to pass was a likely culprit (White et al. 1982; Riley and Fausch 1992; Peterson et al. 2004). Increased effort improved, but did not eliminate, this bias. For 4-pass removal estimates, we attempted use of the generalized removal model that can account for this heterogeneity (Otis et al. 1978); however, the model's goodness-of-fit test typically failed to detect decreased sampling efficiencies. This may be due to the low power of this test for the range of fish abundances within our sites. Accordingly, we do not recommend the generalized model to account for 4-pass sampling efficiency heterogeneity in sites with similar fish abundances.

Confidence intervals around removal estimates rarely encompassed baseline measures of fish abundance. Even though 4-pass estimates were the least biased, confidence intervals were narrower for 3-pass than for 4-pass estimates. This suggests that, in similar cases, the size of a confidence interval around a removal estimate is not a good indicator of its reliability (Hankin and Reeves 1988). In addition, characteristics of our sampling sites affected removal estimate bias. Marked fish removal estimate bias was related to stream size, and when mark-recapture estimates were used as a baseline, stream size and instream wood were related to removal estimate bias. This pattern is similar to what was observed in the sampling efficiency analyses, indicating that what decreases sampling efficiency can, in turn, increase removal estimate bias (also see Peterson et al. 2004).

Readers should bear in mind that our measured sampling efficiencies were low, and removal estimate bias may not be nearly as much of a problem in cases when sampling efficiency is high (e.g., 80% or more). However, the sampling efficiency we observed was not unusually low in the context of similar studies. Although we used pulsed instead of constant direct current to increase electrofishing sampling efficiency (Bohlin et al. 1989), our first-pass measured sampling efficiency fell within the range of unpulsed direct current electrofishing sampling efficiency reported for other salmonids when numbers of marked fish in the site were known (20-57%; Peterson et al. 2004). Our sampling efficiency also fell within the range of sampling efficiencies reported for alternating current electrofishing of warmwater stream fishes when catch was compared to numbers obtained using rotenone adjusted for incomplete capture (7-69% using an electrofisher and electric seine; Bayley and Dowling 1993). Alternating current is more effective than direct current, but has greater potential for fish injury (Bohlin et al. 1989).

Use of models to predict abundances via count data or removal estimates.— Our results suggest that calibration based on sampling efficiency models with habitat covariates and a sufficient amount of sampling effort can be used to reliably predict fish abundance. Direct calibration also successfully corrected catch data and removal estimate bias, and calibration with habitat features taken into account improved model precision.

We used three approaches to model fish abundance: 1) a model of sampling efficiency then used to predict the number of fish in the site (modeled fish abundance = catch/ predicted sampling efficiency), 2) direct calibration of catch data using linear regression, and 3) calibration of biased removal estimates using linear regression with and without site-scale covariates of estimate bias. We observed a strong relationship between unbiased mark-recapture estimates and predicted fish abundance based on sampling efficiency models. This relationship was strongest for models including all 4 electrofishing passes; however, a reasonable level of accuracy could be obtained from low effort models with habitat covariates (Figure 3.1.I 5). This is an encouraging result; many studies that encompass large areas of stream measure fish abundances with single-pass, low effort methods. However, models that directly calibrated catch data without site-scale covariates or models that calibrated biased removal estimates (with and without habitat covariates) were precise ($R^2 > 0.80$) only with catches resulting from the highest level of effort (4 electrofishing passes).

Retrospective calibrations of biased data that consider site-scale covariates of sampling efficiency (e.g., stream size) will be more accurate, particularly if they are applied to low-effort abundance estimates or catch data. Additional variables not considered in this study that may affect sampling efficiency include additional site features (e.g., visibility) and crew ability. The latter is particularly difficult to quantify (e.g., Dunham et al. 2001). To consider crew ability, a consistent designation of crew assignments may be helpful (Dolloff et al. 1993). Alternatively, if this is not possible, calibration models could be based on a broad range of crew assignments, as was done here. This may result in less precise calibrations, but they are likely to apply more broadly among different observers.

Conclusion.—Our objective was to determine the most valid and efficient sampling and calibration approach for our sampling context. An assessment of sampling efficiency and estimate bias at different levels of effort with and without site-scale covariates allowed us to strategize on the most cost-effective way of obtaining reliable abundance data in terms of effort, precision, and bias. It was necessary to use known abundances of marked fish or unbiased mark-recapture estimates as baselines for evaluating sampling efficiency and calibrating removal abundance estimates. Whereas removal estimates were highly correlated for different levels of effort (e.g., single versus multiple-pass removal estimates), all were biased when compared to a valid baseline.

The problem of obtaining a valid approach for sampling fish has led to calls for creation of standardized sampling protocols for entire regions (e.g., states) and habitat types (e.g., ponds and streams) that allow biologists to concentrate resources on improving fish populations instead of routine monitoring considerations (Bonar and Hubert 2002). Whereas there is much value in the concept of standardization, practical implementation will require an understanding of the validity

of estimator assumptions and the range of sampling efficiencies for all species of interest. By definition, a sampling approach that is standardized is one that yields estimates of that have a common meaning (i.e., common uncertainty, expressed as systematic error [bias] and random error [precision]; Taylor and Kuyatt 1994). This view of standardization is one in which use of a common sampling method or protocol is less important than how well and how predictably estimates approximate reality. We recommend routinely using a standard *validation* protocol based in the level of certainty needed to address study objectives. With reliable information on bias and precision of removal (or other) estimates of fish abundance, researchers and managers can determine if population estimates fall within a predetermined 'acceptable' level of error based on research or management objectives, regardless of what sampling approach is used (e.g., Freese 1960; Gregoire and Reynolds 1988).

Acknowledgements

We thank Dona Horan, Joseph Benjamin, Ali Tackett, Lisa Johnstone, Tracie Kirkham, Patrick McKann, Matt Aylsworth, Brooke Nelson, Doug Gibbons, Dan Bolin, Ciara Cusack, Tobias Jongeward, Tim Arrington, Kristin Bott, Aaron Golart, Kristen Bednarczyk, Mary Beatty, and Garet Tessmer for assistance in the field. We also wish to thank Dave Turner, Jim Peterson, and Laura Bond for their assistance in data analysis and interpretation. We thank Jim Peterson, Ashley Steele, Bruce Rieman, Kurt Fausch, and 3 unknown reviewers for helpful comments on earlier versions of this manuscript. Funding for this work was provided by the National Fire Plan and the U.S. Forest Service Rocky Mountain Research Station.

References 3.1.I

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* Second International Symposium on Information Theory. B.N. Petrov and F. Csaki, editors. Akademiai Kiado, Budapest, Hungary.

Bayley, P.B. and D.C. Dowling. 1993. The effects of habitat in biasing fish abundance and species richness estimates when using various sampling methods in streams. Polskie Archiwum Hydrobiologii 40:5-14.

Bohlin, T., S. Hamrin, T.G. Heggberget, G. Rasmussen, and S.J. Saltveit. 1989. Electrofishing – theory and practice with special emphasis on salmonids. Hydrobiologia 173:9-43.

Bonar, S.A. and W.A. Hubert. 2002. Standard sampling of inland fish: benefits, challenges, and a call for action. Fisheries 27:10-16.

Buffington, J.M. and D.R. Montgomery. 1999. A procedure for classifying textural facies in gravel-bed rivers. Water Resources Research 35:1903-1914.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and inference: an information-theoretic approach. Springer-Verlag, New York.

Büttiker, B. 1992. Electrofishing results corrected by selectivity functions in stock size estimates of brown trout (*Salmo trutta* L.) in brooks. Journal of Fish Biology 41:673-684.

Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publications in Statistics 1:131-160.

Dolan, C.R. and L.E. Miranda. 2003. Immobilization thresholds of electrofishing relative to fish size. Transactions of the American Fisheries Society 132:969-976.

Dolloff, C.A., D.G Hankin, G.H. Reeves. 1993. Basinwide estimation of habitat and fish populations in streams. General Technical Report SE-83. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 25pp.

Dunham, J., B. Rieman, and K. Davis. 2001. Sources and magnitude of sampling error in redd counts for bull trout. North American Journal of Fisheries Management 21:343-352.

Freese, F. 1960. Testing accuracy. Forest Science 6:139-145.

Gregoire, T. G. and M. R. Reynolds, Jr. 1988. Accuracy testing and estimation alternatives. Forest Science 34:302-320.

Hankin, D.G. and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834-844.

Joyce, M.P. and W.A. Hubert. 2003. Snorkeling as an alternative to depletion electrofishing for assessing cutthroat trout and brown trout in stream pools. Journal of Freshwater Ecology 18:215-222.

Kruse, C.G., W.A. Hubert, and F.J. Rahel. 1998. Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. North American Journal of Fisheries Management 18:940-946.

Lobón-Cerviá, J. and C.G. Utrilla. 1993. A simple model to determine stream trout (*Salmo trutta* L.) densities based on one removal with electrofishing. Fisheries Research 15:369-378.

Mesa, M.G. and C.B. Schreck. 1989. Electrofishing mark-recapture and depletion methodologies evoke behavioral and physiological changes in cutthroat trout. Transactions of the American Fisheries Society 118:644-658.

Murphy, B.R. and D.W. Willis, editors. 1996. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Mullner, S.A., W.A. Hubert, and T.A. Wesche. 1998. Snorkeling as an alternative to depletion electrofishing for estimating abundance and length-class frequencies of trout in small streams. North American Journal of Fisheries Management 18:947-953.

Myers, R.H. 1990. Classical and modern regression with applications, 2nd edition. Duxbury Press, Belmont, California.

Otis, D.L., K.P. Burnham, G.C. White, and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1-135.

Overton, K.C., S.P. Wolrab, B.C. Roberts, and M.A. Radko. 1997. R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory procedures handbook. General Technical Report INT-GTR-346. Ogden, Utah: USDA Forest Service: 72pp.

Peterson, J.T., R.F. Thurow, and J.W. Guzevich. 2004. An evaluation of multi-pass electrofishing for estimating the abundance of stream-dwelling salmonids. Transactions of the American Fisheries Society 113:462-475.

Riley, S.C. and K.D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. North American Journal of Fisheries Management 12:768-776.

Riley, S. C., R.L. Haedrich, and R. Gibson. 1993. Negative bias in removal estimates of Atlantic salmon parr relative to stream size. Journal of Freshwater Ecology 8:97-101.

Rodgers, J.D., M.F. Solazzi, S.L. Johnson, and M.A. Buckman. 1992. Comparison of three techniques to estimate juvenile Coho salmon populations in small streams. North American Journal of Fisheries Management 12:79-86.

Royall, R.M. 1997. Statistical evidence: a likelihood paradigm. Chapman and Hall, New York.

Simonson, T.D. and J. Lyons. 1995. Comparison of catch per effort and removal procedures for sampling stream fish assemblages. North American Journal of Fisheries Management 15:419-427.

Simpson, D.E. 1978. Evaluation of electrofishing efficiency for largemouth bass and bluegill populations. Master's Thesis. University of Missouri, Columbia, Missouri, USA.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research, 3rd ed. W.H. Freeman and Company, New York.

Taylor, B.N. and C.E. Kuyatt. 1994. Guidelines for evaluating and expressing the uncertainty of NIST measurement results. National Institute of Standards and Technology technical note 1297, Gaithersburg, MD. 24pp.

Thompson, W.L. 2003. Hankin and Reeves' approach to estimating fish abundance in small streams: limitations and alternatives. Transactions of the American Fisheries Society 132:69-75.

Thompson, W.L., G.C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego.

Thurow, R.F. and D.J. Schill. 1996. Comparison of day snorkeling, night snorkeling, and electrofishing to estimate bull trout abundance and size structure in a second-order Idaho stream. North American Journal of Fisheries Management 16:314-323.

Williams, L.R., M.L. Warren, Jr., S.B. Adams, J.L. Arvai, and C.M. Taylor. 2004. Basin visual estimation technique (BVET) and representative reach approaches to wadeable stream surveys: methodological limitations and future directions. Fisheries 29: 12-22.

White, G.C., D. R. Anderson, K.P. Burnham, and D.L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory report number LA-8787-NERP, Los Alamos, New Mexico.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82-90.

TABLE 3.1.1.1.—Characteristics of 31 study sites in headwater tributaries of the Boise River and Panther Creek, Idaho sampled to estimate fish abundance in 2002-2003.

Variable	Mean	SD	Range
Site elevation (m)	1511	208	1134 – 2034
Site length (m)	103.9	8.7	90.0 - 132.9
Mean wetted width (m)	2.9	0.9	1.5 - 4.8
Mean depth (m)	0.10	0.03	0.06 - 0.15
Mean cross-sectional area (m^2)	0.32	0.16	0.10 - 0.63
Conductivity (μs)	49.6	26.8	11.1 - 116.0
Temperature (degrees C)	12.9	3.3	7.2 - 20.0
Gradient	0.06	0.03	0.004 - 0.14
Total length undercut banks (m)	5.5	8.9	0 - 41.2
Instream wood (total count)	17	16	0 - 64
Substrate (% composition)			
Fine	3.4	4.8	0 - 19.9
Sand	9.0	6.8	0 - 24.1
Gravel	31.3	17.8	6.4 - 80.2
Cobble	30.9	12.3	0.7 – 53.4
Boulder	25.4	13.8	0 - 50.0
Embedded	16.1	9.9	0 - 34.2
Median length of fish > 60 mm (mm)	105	21	72-136
Recovery period after marking (h)	24.0	7.0	15.4 - 47.3

TABLE 3.1.I 2.—Parameter estimates for best-fitting logistic regression models of overall sampling efficiency based on (a) known numbers of marked fish released in a site (measured sampling efficiency) and (b) mark-recapture abundance estimates (mark-recapture sampling efficiency). Sites were located in headwater tributaries of the Boise River and Panther Creek, Idaho and sampled in 2002-2003 (CL = confidence limit).

(a)

Measured sampling efficiency

	Parameter estimate	Lower 95% CL	Upper 95% CL
Intercept	1.62	2.25	1.02
Log_{10} mean cross-sectional area	-2.09	-3.73	-0.46

(b)

Mark-recapture sampling efficiency

	Parameter estimate	Lower 95% CL	Upper 95% CL
Intercept	0.61	-1.05	2.28
Log_{10} mean cross-sectional area	-1.58	-3.51	0.35
Mean temperature	-0.02	-0.14	0.10
Median length	0.01	-0.01	0.03

TABLE 3.1.I 3.—Model-averaged parameter estimates for best-fitting linear regression models of 4-pass removal estimate bias based on (a) known numbers of marked fish released in a site and (b) mark-recapture abundance estimates. Sites were located in the Boise River and Panther Creek, Idaho and sampled in 2002-2003 (CL = confidence limit).

(a) 4-pass marked fish removal estimate bias (% numbers of marked fish released)

	Parameter Estimate	Lower 95% CL	Upper 95% CL
Intercept	0.639	0.315	0.962
Log_{10} mean cross-sectional area	-0.463	-0.787	-0.139
Log_{10} total length undercut bank	0.006	0.000	0.011
Log_{10} instream wood	-0.003	-0.005	0.000
% Cobble substrate	0.002	-0.001	0.005
Mean temperature	-0.004	-0.010	0.002
Median trout length	0.003	0.000	0.005

(b) 4-pass removal estimate bias (% mark-recapture estimate)

	Parameter Estimate	Lower 95% CL	Upper 95% CL
Intercept	0.970	0.716	1.225
Log_{10} mean cross-sectional area	-0.358	-0.671	-0.045
Log_{10} total length undercut bank	0.006	-0.002	0.013
Log_{10} instream wood	-0.008	-0.011	-0.004
% Cobble substrate	-0.002	-0.006	0.003
Mean temperature	0.001	-0.002	0.003
Median trout length	0.000	0.000	0.001

TABLE 3.1.I 4.—A summary of logistic regressions for predicting cumulative sampling efficiencies of rainbow trout after 1, 2, 3, or 4 electrofishing passes in sites sampled in 2002-2003 within the Boise River and Panther Creek, Idaho. Leave-one-out predictions from these models were used to generate predictions of fish abundance estimates in Figure 3.1.I 5 (CL = confidence limit).

	Parameter Estimates (lower and upper CL)			
Variables	4-pass	3-pass	2-pass	1-pass
Intercept	1.47 (0.53, 2.48)	1.25 (0.36, 2.19)	0.61 (-0.17, 1.42)	-0.31 (-1.02, 0.39)
Log_{10} mean cross-sectional area	-0.51 (-1.04, 0.004)	-0.31 (-0.80, 0.18)	-0.37 (-0.81, 0.06)	-0.35 (-0.74, 0.04)
Log_{10} instream wood	-0.47 (-0.72, -0.24)	-0.39 (-0.62, 0.17)	-0.35 (-0.54, -0.15)	-0.26 (-0.43, -0.09)

TABLE 3.1.I 5.— Linear regression models predicting mark-recapture estimates based on cumulative catch after 1, 2, 3, and 4 passes in sites sampled in 2002-2003 within the Boise River and Panther Creek, Idaho. Prediction sum of squares (PRESS) residuals indicate relative model predictive performance using a leave-one-out validation approach and were used to generate R^2_{Pred} that reflects prediction capabilities of models (Myers 1990; CL = 95% confidence limit).

	Parameter Estimates (lower and upper CL)			
Variables	4-pass	3-pass	2-pass	1-pass
Intercept	-0.07 (-7.42, 7.28)	1.05 (-6.83, 8.92)	2.81 (-6.18, 11.79)	6.25 (-3.45, 15.95)
Cumulative Catch	1.43 (1.20, 1.66)	1.51 (1.24, 1.78)	1.70 (1.33, 2.07)	2.25 (1.68, 2.82)
R^2_{pred}	0.82	0.78	0.72	0.64

TABLE 3.1.I 6.—Pearson's *r* correlation matrix between biased 4-, 3-, and 2-pass removal estimates and validated mark-recapture population estimates of rainbow trout within sites in headwater tributaries of the Boise River and Panther Creek, Idaho sampled in 2002-2003.

Fish abundance estimates	2-pass removal	3-pass removal	4-pass removal
2-pass removal estimate	-	0.76	0.70
3-pass removal estimate	0.76	-	0.89
4-pass removal estimate	0.70	0.89	-
Mark-recapture estimate	0.61	0.75	0.84

TABLE 3.1.I 7.—Linear and multiple-regression models predicting mark-recapture estimates based on 4-, 3-, and 2-pass removal estimates in sites sampled in 2002-2003 within the Boise River and Panther Creek, Idaho, with (a) and without (b) site-scale habitat covariates included in the models. Prediction sum of squares (PRESS) residuals were used to generate R^2_{Pred} that reflects leave-one-out prediction capabilities of models (Myers 1990; CL = 95% confidence interval).

a)

	Parameter Estimates (lower and upper CL)		
Variables	4-pass	3-pass	2-pass
Intercept	-9.7, (-19.7, 0.27)	-5.6, (-20.6, 9.5)	-1.2, (-18.7, 16.3)
Abundance estimate	1.3, (1.1, 1.4)	1.3, (1.0, 1.6)	1.0, (0.7, 1.3)
Log_{10} cross-sectional area	-2.0, (-4.4, 0.4)	0.6, (-3.1, 4.3)	1.5, (-3, 5.9)
Log_{10} instream wood	4.3, (1.2, 7.4)	4.4, (-0.3, 9)	7.3, (1.8, 12.8)
R^2_{pred}	0.85	0.56	0.40

b)

	Parameter Estimates (lower and upper CL)		
Variables	4-pass	3-pass	2-pass
Intercept	1.5, (-5.6, 8.7)	4.2, (-6.1, 14.5)	17.4, (6.4, 28.1)
Abundance estimate	1.3, (1.1, 1.5)	1.3, (1.0, 1.6)	0.9, (0.6, 1.2)
R^2_{pred}	0.83	0.65	0.40

Figure descriptions (3.1.I)

FIGURE 3.1.I 1.—Box plots of electrofishing sampling efficiency over 4 consecutive depletion passes, expressed as measured sampling efficiency (% recapture of a known number of marked fish released into the site minus escapement) and removal model sampling efficiency (calculated using the program CAPTURE; Otis et al. 1978; White et al. 1982).

FIGURE 3.1.I 2.—Abundance of marked rainbow trout in 36 sites in Boise River and Panther Creek tributaries sampled in 2002-2003, expressed as known numbers of marked fish released and 4-, 3-, and 2-pass marked fish removal estimates with 95% confidence intervals. Lines indicate magnitude of removal estimate bias (estimate – marked fish released).

FIGURE 3.1.I 3.—Abundance of rainbow trout > 60 mm in 38 sites in the Boise River and Panther Creek tributaries sampled in 2002-2003, expressed as mark-recapture estimates and 4-, 3-, and 2-pass removal estimates with 95% confidence intervals. Lines indicate magnitude (*n*) of difference between the two estimates (removal estimate - mark-recapture estimate).

FIGURE 3.1.I 4.—The relationship between mark-recapture abundance estimates and predicted fish abundance based on logistic regression models (predicted abundance = known catch/ predicted sampling efficiency). Predictions are based on a leave-one-out validation approach, and error bars represent prediction intervals around the estimate. Separate models were constructed for each level of sampling effort (1-, 2-, 3-, and 4-pass cumulative catch). Equations for best-fitting trend lines and R^2 values are also presented.

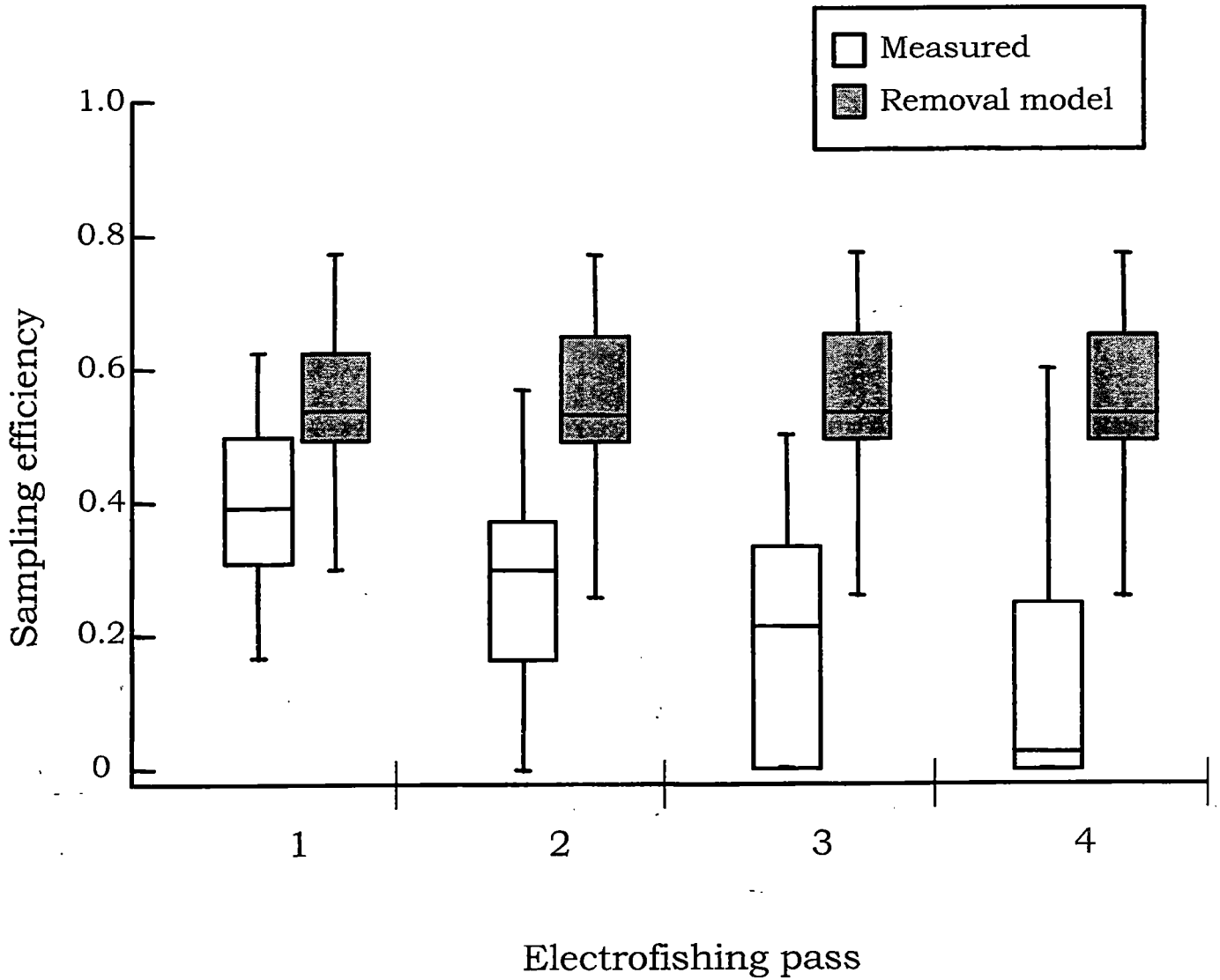


Figure 3.1.I 1

Figure 2

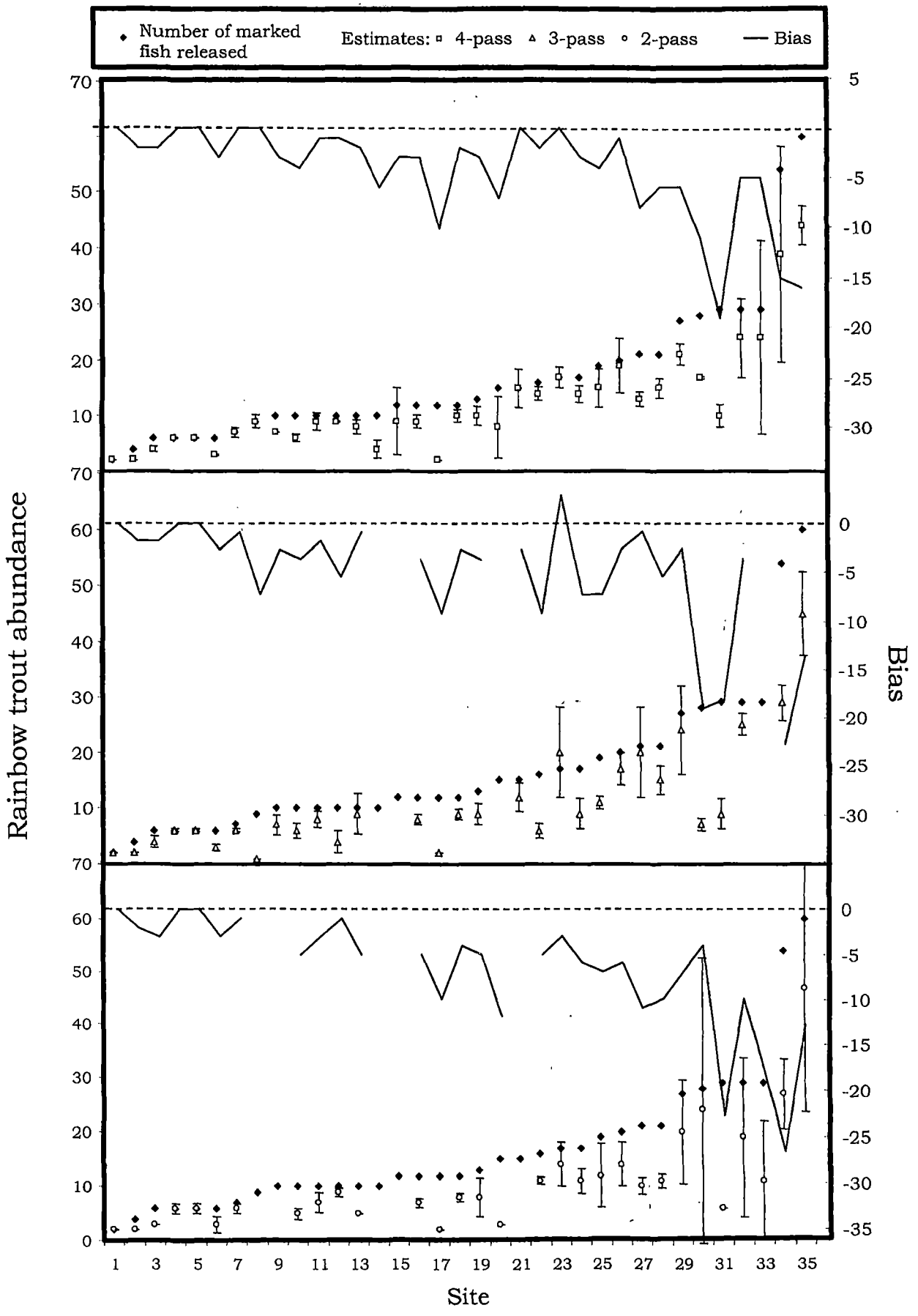

Number of marked fish released
Estimates: 4-pass 3-pass 2-pass
Bias
Rainbow trout abundance
Bias
Site

Figure 3.1.1 2

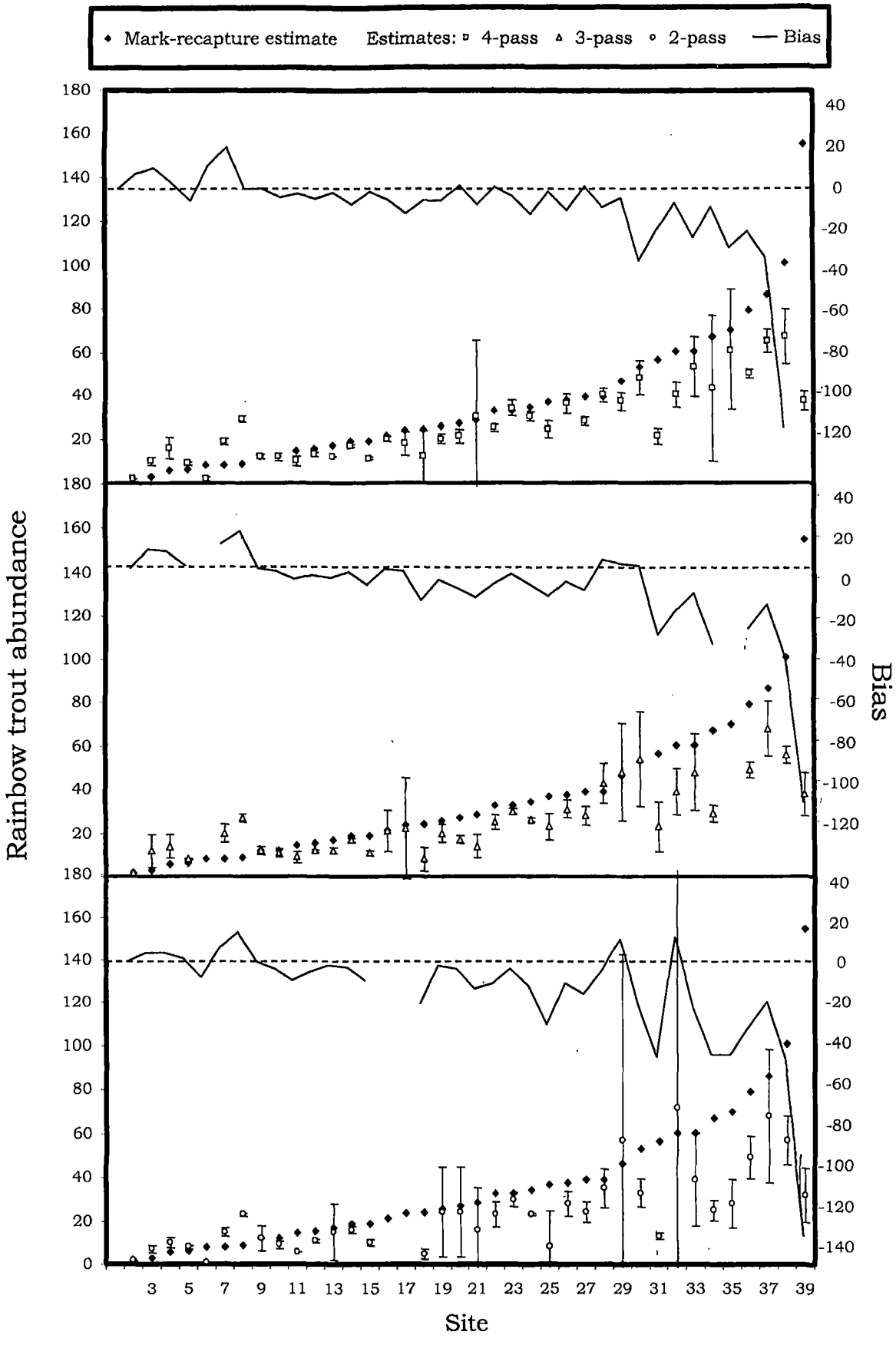


Figure 4

Figure 3.1.1

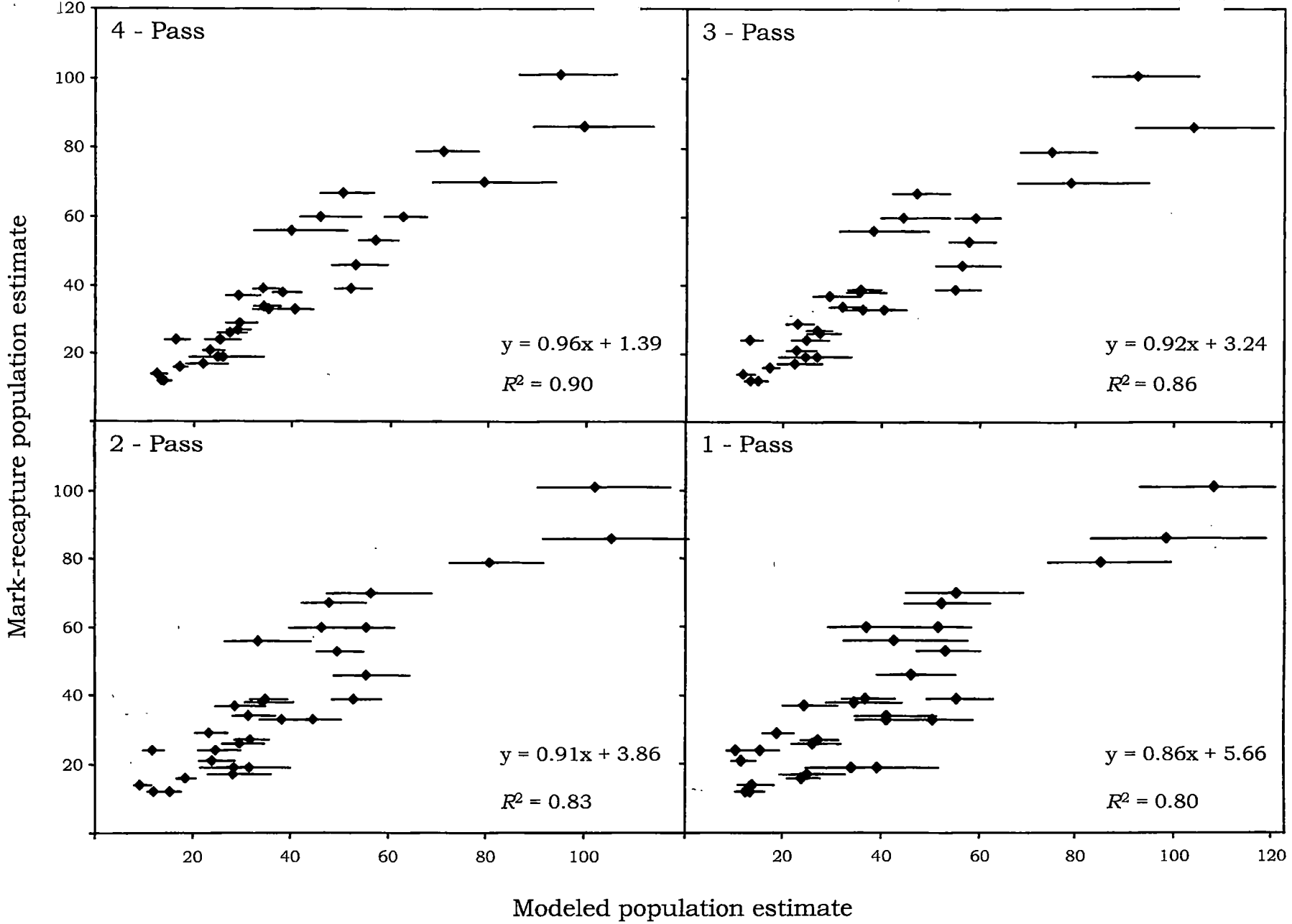

4 - Pass
y = 0.96x + 1.39
R^2 = 0.90
3 - Pass
y = 0.92x + 3.24
R^2 = 0.86
2 - Pass
y = 0.91x + 3.86
R^2 = 0.83
1 - Pass
y = 0.86x + 5.66
R^2 = 0.80
Mark-recapture population estimate
Modeled population estimate
20
40
60
80
100
120

Figure 3.1.I 4

RESEARCH AREA 3 * GOAL 1 * PUBLICATION II:

Validation of endoscopy for determination of maturity of small salmonids and sex of mature individuals

Abstract.— Fish maturity, sex ratio, and age and/or size at first maturity are important parameters in population assessments and life history studies. In most empirical studies of these parameters, fish are sacrificed and dissected to obtain data. However, maturity and the sex of mature individuals can be determined by inserting an endoscope through a small incision in the body cavity wall and viewing the gonads. The objective of this study was to evaluate endoscopy in a field setting for gonadal assessment of stream resident forms of salmonids that mature at small sizes. Ninety-one brook trout *Salvelinus fontinalis* (60-210 mm) were obtained via electrofishing and anaesthetized. Maturity and sex of mature individuals were determined using an endoscope. After recovery, individuals were euthanized with anesthetic and dissected to validate the endoscopic classification. Endoscopy correctly determined the maturity and sex of mature individuals for 96% of the brook trout, with the highest accuracy observed for the smallest (60-70 mm) and largest (>140 mm) individuals examined. In the misclassifications, visceral fat hampered visibility and was mistaken for mature testes. Immediate post-procedure mortality was 3.3% and limited to individuals smaller than 70 mm in fork length. Endoscopy is a useful technique that can be used in field settings to assess maturity and sex of mature fish with a low rate of immediate mortality.

Introduction

To effectively conserve fish populations, it is critical to understand mechanisms that contribute to population dynamics and resilience to disturbance, such as life history diversity. Important parameters used in population assessments and life history studies include sex ratio, maturity, and age and size at first maturity (e.g., Meerburg 1986). We wished to identify a technique to accurately obtain these data from small, resident salmonids (50-250 mm) that would allow the fish to be collected, examined, and released in the field with a low risk of mortality. External characteristics that indicate maturity or sex (e.g., kype, gametes produced by pressing gonads) are not consistently apparent in small salmonids, particularly prior to the latter stages of gonadal development (e.g., Martin et al. 1995). Without such reliable external characteristics, fish have been typically sacrificed to obtain these data (Fleming 1998; Kennedy et al. 2003; Meyer et al. 2003).

We evaluate endoscopy as an alternative approach. Endoscopy is used in medical and veterinary settings to view internal organs via insertion of the instrument into the body cavity through a small incision (e.g., Wildhaber et al. 2005) or through the urogenital pore (e.g., Ortenburger et al. 1996). The endoscope consists of a thin tube (in our case, 2.7 mm in diameter) containing fiber optics to transmit light from an external source for illumination of internal organs, which are viewed through an eyepiece or video camera attached to the tube. As with any surgical procedure, there are risks to subject organisms, but they are generally very low with endoscopy (e.g., Froehlich et al. 1999). Otoscopes (designed for viewing the human ear) and endoscopes have been successfully used as a generally non-lethal method of determining the sex and/or maturity of fish in laboratory settings, including European catfish *Silurus glanis* (Fijan 1975), largemouth bass *Micropterus salmoides* (Driscoll 1969), rainbow trout *Oncorhynchus mykiss* (Steucke and Atherton 1965; Moccia et al. 1984), Arctic char *Salvelinus alpinus* (Ortenburger et al. 1996), and shovelnose sturgeon *Scaphirhynchus platorynchus* (Wildhaber et al. 2005). Endoscopy has also been used in the field to assess maturity and sex of small, stream-resident forms of bull trout (100-250 mm) *Salvelinus confluentis*, a species listed as threatened under the U.S. Endangered Species Act (P. Howell, unpublished data), and small rainbow trout (54-217 mm; E. Swenson, unpublished data).

A variety of techniques besides endoscopy are available to non-lethally determine the maturity and sex of fish; however, some approaches are costly or are limited to laboratory settings. For example, ultrasound has been employed for these purposes (e.g., Evans et al. 2004; Bryan et al. 2005); however, relatively high cost of the equipment may limit its use. For example, an endoscope and related equipment cost approximately $4,000, whereas a portable ultrasound unit costs $13,000-$18,000. Blood plasma indicators can also be useful, but this technique is highly invasive (Webb et al. 2002) and cannot be non-lethally sampled in fish less than 150 mm (Strange 1996).

The primary purpose of this study was to validate the use of endoscopy to determine whether small salmonids were maturing or mature (hereafter, mature) and to determine the sex of mature individuals. We applied the technique to eastern brook trout *Salvelinus fontinalis* (approximately 60-200 mm fork length). Brook trout is nonnative to the study area (Boise River system, Idaho) and, consequently, could be sacrificed to verify endoscopic classifications without raising

conservation concerns. In this region, brook trout appear to spawn at small sizes, similar to that observed for other small, resident forms of salmonids in the area (e.g., rainbow trout; A. Rosenberger, unpublished data). Our intent was not to identify stages or gradations of maturity (e.g., Wildhaber et al. 2005), but whether fish were ripening during late summer prior to the spawning season in the fall. Specific objectives were to use endoscopy in the field to 1) classify brook trout as immature or mature and 2) distinguish the sex of mature fish; we also 3) validated endoscopic classifications by dissection of the same fish and 4) determined the extent of immediate (but not long-term) mortality associated with the procedure.

Methods

Brook trout were collected from Beaver Creek, a tributary to the Crooked River in the Boise River drainage in southwestern Idaho. Sampling using a Smith-Root backpack electrofisher (LR-24 or 12B Electrofisher, Vancouver, WA) with pulsed direct current (DC) took place on August 5, 2005, prior to the fall reproductive season for this species. Voltage, pulse, and frequency were adjusted to maximize capture probability with minimal fish injury (settings range: voltage = 400-700, frequency = 30-50 Hz, pulse width = 2-8 ms). Once captured, fish were held in live wells containing ambient stream water outside the influence of the electrofishing unit.

The endoscope operator had prior experience using endoscopy on wild rainbow trout (A. Rosenberger, unpublished data). However, 10 brook trout were initially used to re-acquaint the operator with the procedure. After endoscopy, these individuals were humanely euthanized and dissected to reorient the operator with the location and appearance of the peritoneal organs, particularly the gonads, which vary in color and seasonal development among trout and char species. After this initial training, 91 individual brook trout were examined for this study.

Individual fish were removed from live wells and placed in a tub filled with stream water and the minimum amount of tricaine methanesulfonate (MS 222) needed for a fish to lose equilibrium within 5 min. Fish were then moved to a small, portable platform, placed on their side, and measured for fork length to the nearest mm. During the endoscopy procedure, the operator practiced standard aseptic techniques while an assistant irrigated gills every 30 to 40 seconds by injecting water with anethestic into the mouth using a 10 ml syringe. A small, 3-5 mm, incision was made directly above the pelvic hius on the left side of the fish for insertion of the endoscope into the body cavity. To improve visibility, 10% saline solution was injected into the peritoneum until excess solution began to seep out of the incision. The fish was then gently held by the operator while viewing the gonads. The endoscope was a rigid Richard Wolf® 25 degree, Panoview Plus (item number 8672.412) equipped with a fiber optic light source (WelchAllyn Solarc Light Source® LB-21) powered by a 7 Ah 12 volt battery.

Gonads were categorized as mature or immature, and, if mature, the sex of the individual was determined, using categories similar to Bonar et al. (1989) in a study validating the use of ultrasound for identifying sex and maturity of Pacific herring. Previous use of this technique and dissection indicated that identification of the sex of immature gonads in other small salmonids is difficult; and, therefore, the classification of immature individuals as male or female was likely unreliable. Consequently, the sex of immature fish in this study was not documented.

After the endoscope was removed from the fish, the fish was returned to the portable platform. The incision was closed with Nexaband® surgical glue (usually a drop). If the incision appeared large or likely to open, the operator also used a nylon suture to close the wound. On average, the endoscopy procedure lasted 4 min. Fish identified as mature were then marked with an upper or lower caudal fin clip to indicate sex and placed in a recovery bucket filled with water at ambient stream temperatures. After sufficient time had passed to assess initial recovery of individuals (fish swimming unaffectedly in holding bucket), they were euthanized with MS 222 and dissected to validate the endoscopic classifications through direct examination of the gonads (Crim and Glebe 1990).

Results and Discussion

We found endoscopy to be a highly accurate method for determining maturity and sex of mature brook trout. Of the 91 fish examined using endoscopy and dissected for validation, 96% ($n = 87$) were correctly classified as immature or mature (Table 3.1.IIs 1 and 2). Similarly, the sex of 96% (27 of 28) of the mature adults was correctly classified. Mature females had pale, yellow-colored eggs approximately 3-5 mm in diameter in ovaries running the entire length of the body cavity. For mature males, long, highly vascularized, opaque, and smooth, milky white testes were visible along the length of the body cavity. Immature individuals had small, thin, transparent or translucent gonads. Occasionally, small, grain-sized (~1 mm), developing oocytes were observed in immature individuals. However, we were able to distinguish these small oocytes from larger eggs of mature females. Through the endoscope, individual or multiple developing oocytes were easily viewed in their entirety and semi-transparent, whereas an egg was typically similar to or larger than the field of view and more opaque.

Overall accuracy for both maturity and sex classifications was highest for the smallest and largest size classes (Table 3.1.II 1). Misidentification of fat stores as mature testes was the cause of endoscope error. Misclassification of immature fish as mature males accounted for error in maturity classifications, and one mature female was incorrectly classified as male (Table 3.1.II 2). This may be a common source of error using this procedure; the ability of the endoscope to distinguish between fat and testes was limited in endoscopic studies of sturgeon (Wildhaber et al. 2005). Endoscopy could introduce bias in comparative maturity data between locations where fish differ in condition. In addition to fat stores, full stomachs occasionally impeded visibility of gonads. Evacuation of stomach contents prior to the endoscopy could eliminate this source of error. Regardless, the accuracy evident in our results support other studies that indicate that endoscopy is a useful technique for determining maturity and sex of mature fish (Moccia et al. 1984; Ortenburger et al. 1996; Wildhaber et al. 2005) and, further, suggests that its use can be expanded to individuals that mature at relatively small sizes (80-100 mm).

In addition, risk of immediate mortality from the procedure appears to be low. Three of the 91 fish (3.3%) that underwent endoscopy died prior to euthanization for dissection (Table 3.1.II 1). These were 60-70mm in fork length, the smallest size class examined. In smaller individuals, it was more difficult to view the internal organs, and the gonads were much less apparent in immature fish. As a result, the procedure may have taken longer. In addition, in smaller fish, the incision is larger relative to body size. Although the specific cause of mortality was uncertain and could include factors not directly related to the endoscopy (e.g., electrofishing, reaction to

anesthesia), smaller individuals may be at greater risk from this procedure than larger fish. The relationship between fish size and risk of mortality from the procedure may be an important consideration when using this technique on rare fishes. If the technique is primarily used to determine the sex of mature fish rather than timing of maturity, endoscopy can be limited to larger individuals most likely to be mature. To avoid bias, this would require prior data collection regarding minimum size at maturity for males and females.

Although mortality shortly after this procedure may be low, this study does not rule out the possibility of delayed complications, such as re-opening of the incision, infection, and injury to internal organs. Incidental loss of epidermal mucus, increases in body temperature, and/or drying of the skin could contribute to eventual mortality in fish that undergo the procedure. Previous study indicates that this is unlikely; Moccia et al. (1984) noted that necropsy of fish maintained under controlled laboratory conditions revealed no evidence of internal damage from endoscopy such as internal bruising or infection, and, without antibiotics, entry incisions healed a week after application of tissue adhesive. However, fish released into wild settings after endoscopy may be more susceptible to these and other sources of related mortality, such as subsequent predation. Further study is needed to evaluate the long-term lethal and sublethal effects of endoscopy in natural settings. However, examinations of radio tagging, a procedure more invasive than endoscopy, suggest that these problems may be minimal. Radio tags in largemouth bass *Micropterus salmoides* and dummy acoustic transmitters in juvenile Atlantic salmon *Salmo salar* had few long-term effects on fish in the wild (Cooke et al. 2003; Lacroix et al. 2004).

The endoscope was determined to be a useful tool for identifying maturity of small brook trout and the sex of mature fish with a low rate of immediate mortality. The equipment is compact, portable, and, with exception of the light source, water resistant. These characteristics make it practical for field applications, even in remote settings. However, endoscopy requires knowledge of fish anatomy and experience observing gonads at various stages of development. This could potentially lead to operator-to-operator differences in error. Gonadal and gametic differences among species, such as size, color, and seasonal development should also be considered. Prior to using this technique for scientific study, training and validation may minimize operator error as well as incidental injury or mortality to the fish. In addition, endoscopy can be useful for purposes other than observing sexual organs. The spleen, liver, visceral fat, and intestinal tract were also observed through the endoscope (see also Moccia et al. 1984).

Acknowledgements

Funding for this work was provided by the National Fire Plan; the U.S.D.A. Forest Service Rocky Mountain Research Station, Boise Aquatic Sciences laboratory; and the Bonneville Power Administration. Thanks to Joe Benjamin and Aubrey Bower for assistance in the field. We also thank Chris Walser, Jason Dunham, Sara Heggland, Jacqui Hall, Sam Brenkman, and two anonymous reviewers for helpful comments on earlier versions of this manuscript.

References 3.1.II

Bonar, S. A., G. L. Thomas, G. B. Pauly, and R.W.Martin. 1989. Use of ultrasonic images for rapid nonlethal determination of sex and maturity of Pacific herring. North American Journal of Fisheries Management 9:364–366.

Bryan, J.L., M.L. Wildhaber, and D.B. Noltie. 2005. Examining Neosho madtom reproductive biology using ultrasound and artificial photothermal cycles. North American Journal of Aquaculture 67:221–230.

Cooke, S.J., B.D.S. Graeb, C.D. Suski, and K.G. Ostrand. 2003. Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: case study of a novice and experienced fish surgeon. Journal of Fish Biology 62:1366-1380.

Crim, L.W. and B.D. Glebe. 1990. Reproduction. Pages 529-547 *in* C.B. Schreck and P.B. Moyle, editors. Methods for Fish Biology. American Fisheries Society, Bethesda, Maryland.

Driscoll, D.P. 1969. Sexing the largemouth bass with an otoscope. Progressive Fish Culturalist 31:183-184.

Evans, A.F., M.S. Fitzpatrick, and L.K. Siddens. 2004. Use of ultrasound imaging and steroid concentrations to identify maturational status in adult steelhead. North American Journal of Fisheries Management 24:967–978.

Fijan, N. 1975. Induced spawning, larval rearing and nursery operations--*Silurus glanis*. Workshop on Controlled Reproduction of Cultivated Fishes, Hamburg, 21-25 May 1973, EIFAC/T25:130-138.

Fleming, I. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Canadian Journal of Fisheries and Aquatic Sciences 55:59-76.

Froehlich F., J.J. Gonvers , J.P. Vader, R.W. Dubois, and B. Burnand. 1999. Appropriateness of gastrointestinal endoscopy: Risk of complications. Endoscopy 31:684-686.

Kennedy, B.M., D.P. Peterson, and K.S. Fausch. 2003. Different life histories of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. Western North American Naturalist 63:215-223.

Lacroix, G.L., D. Knox, and P. McCurdy. 2004. Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. Transactions of the American Fisheries Society 133:211-220.

Martin, S.W., J.A. Long, and T.N. Pearsons. 1995. Comparison of survival, gonad evelopment, and growth between rainbow trout with and without surgically implanted dummy radio transmitters. North American Journal of Fisheries Management 15:494-498.

Meerburg, D.J., editor. 1986. Salmonid age at maturity. Canadian special publication of fisheries and aquatic sciences 89. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Meyer, K.A., D.J. Schill, F.S. Elle, and J.A. Lamansky. 2003. Reproductive demographics and factors that influence length at sexual maturity of yellowstone cutthroat trout in Idaho. Transactions of the American Fisheries Society 132:183-195.

Moccia, R.D., E.J. Wilkie, K.R. Munkittrick, and W.D. Thompson. 1984. The use of fine needle fibre endoscopy in fish for in vivo examination of visceral organs, with special reference to ovarian evaluation. Aquaculture 40:255-259.

Ortenburger, A.I., M.E. Jansen, and S.K. Whyte. 1996. Nonsurgical videolaproscopy for determination of reproductive status of the Arctic charr. Canadian Veterinary Journal 37:96-100.

Steucke, E.W. and C.R. Atherton. 1965. Use of microhematocrit values to sex largemouth bass. Progressive Fish Culturist 27:87-90.

Strange, R.J. 1996. Field examination of fishes. Pages 433-446 *in* B.R. Murphy and D.W. Willis, editors. Fisheries Techniques, second edition. American Fisheries Society, Bethesda, MA.

Webb, M.A.H., G.W. Feist, E.P. Foster, C.B. Schreck, and M.S. Fitzpatrick. 2002. Potential classification of sex and stage of gonadal maturity of wild white sturgeon using blood plasma indicators. Transactions of the American Fisheries Society 131:132–142.

Wildhaber, M.L., D.B. Papoulias, A.J. DeLonay, D.E. Tillitt, J.L. Bryan, M.L. Annis, and J.A. Allert. 2005. Gender identification of shovelnose sturgeon using ultrasonic and endoscopic imagery and the application of the method to pallid sturgeon. Journal of Fish Biology 67: 114-132.

TABLE 3.1.II. 1—Maturity and sex of mature brook trout captured from Beaver Creek, Boise River Basin, Idaho. The number of immature, mature female, and mature male brook trout in each size class determined endoscopically is followed parenthetically by the number determined by dissection.

Fork Length (mm)	Total	Mortalities	Female	Male	Immature
60-70	43	3	0 (0)	0 (0)	43 (43)
71-120	12	0	0 (0)	4 (2)	8 (10)
121-140	19	0	1 (1)	12 (10)	6 (8)
141-209	17	0	7 (8)	8 (7)	2 (2)
All Size Classes	91	3	8 (9)	24 (19)	59 (63)

TABLE 3.1.II 2.—Contingency table summarizing the accuracy of endoscopy for determining maturity and sex of mature brook trout captured from Beaver Creek, Boise River Basin, Idaho.

	Endoscope		
Dissection	Immature	Mature Females	Mature Males
Immature	59	0	4
Mature Females	0	8	1
Mature Males	0	0	19

GOAL 2: UNDERSTAND RESPONSES OF KEY HABITAT VARIABLES TO FIRE (CHANNEL STRUCTURE, DYNAMICS, AND STREAM TEMPERATURE), BETTER UNDERSTAND KEY ENVIRONMENTAL GRADIENTS AND HOW THEY ARE DISTRIBUTED ACROSS THE LANDSCAPE, AND RELATE TO AQUATIC VERTEBRATE DISTRIBUTIONS ACROSS THE BASIN.

We have 1 manuscript that has been published and 1 in preparation under this goal:

1. Dunham, J.B., A.E. Rosenberger, C.H. Luce, and B.E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems* 10:335-346.
2. Rosenberger, A.E., J.B. Dunham, M.S. Wipfli, and J.M. Buffington. in prep. Effects of wildfire and channel reorganization on drifting macroinvertebrates and predation by trout in central Idaho streams a decade after disturbance. To be submitted to *Transactions of the American Fisheries Society.*

We have also completed an analysis of the effects of wildfire and channel-reorganizing events on channel morphology (Buffington, unpub.).

The following sections contain the content of these two manuscripts and the analysis.

RESEARCH AREA 3 * GOAL 2 * PUBLICATION I

Influences of Wildfire and Channel Reorganization on Spatial and Temporal Variation in Stream Temperature and the Distribution of Fish and Amphibians

Abtract.—Wildfire can influence a variety of stream ecosystem properties. We studied stream temperatures in relation to wildfire in small streams in the Boise River basin, located in central Idaho, USA. To examine the spatio-temporal aspects of temperature in relation to wildfire, we employed three approaches: a pre-post fire comparison of temperatures between two sites (one from a burned stream and one unburned) over 13 years, a short-term (3 year) pre-post fire comparison of a burned and unburned stream with spatially extensive data, and a short-term (1 year) comparative study of spatial variability in temperatures using a "space for time" substitutive design across 90 sites in nine streams. The latter design included streams with a history of stand-replacing wildfire and streams with severe post-fire reorganization of channels due to debris flows and flooding. Results from these three studies indicated that summer maximum water temperatures can remain significantly elevated for at least a decade following wildfire, particularly in streams with severe channel reorganization. In the retrospective study we investigated occurrence of native rainbow trout (*Oncorhynchus mykiss*) and tailed frog larvae (*Ascaphus montanus*) in relation to maximum stream temperatures during summer. Both occurred in nearly every site sampled, but tailed frog larvae were found in much warmer water than previously reported in the field (26.6 °C maximum summer temperature). Our results show that physical stream habitats can remain altered (e.g., increased temperature) for many years following wildfire, but that native aquatic vertebrates can be resilient. In a management context, this suggests wildfire may be less of a threat to native species than human influences that alter the capacity of stream-living vertebrates to persist in the face of natural disturbance.

Introduction

Wildfire is a major source of natural disturbance in stream ecosystems (McMahon and deCalesta 1990; Minshall and others 1997; Gresswell 1999). Some of the most dramatic disturbances from wildfire involve post-fire flooding and debris flows. These events completely reorganize channels by redistributing massive amounts of sediment and wood that scour and fill different portions of stream channel networks (Benda and others 2003; Meyer and Pierce 2003; Miller and others 2003; Wondzell and King 2003). In the short-term, these events can lead to massive mortality of benthic macroinvertebrates (Minshall 2003), amphibians (Pilliod and others 2003; Bury 2004), and fishes (Rieman et al. 1997; Burton 2005). Over time, stream biota can recover and some responses of benthic macroinvertebrates suggest that community structure begins to stabilize within 7-10 years following wildfire (Minshall 2003; but see Rosenberger and others 2006 [companion paper]). The rate and nature of recovery of fishes and amphibians is likely dependent on characteristics of the species and the disturbed habitat (Dunham and others 2003; Pilliod and others 2003). Wildfire is a natural process and perhaps less of a threat in unmanaged ecosystems (e.g., wilderness areas), but the vulnerability of many species to fire-related disturbances has increased due to human influences on aquatic vertebrates and altered fire regimes (Minshall 2003).

Although some groups of organisms appear to have the capacity to recover within several years of wildfire and related disturbances, the extent, magnitude, and duration of many important physical changes to stream environments and their specific influences on stream biota are still poorly understood (Gresswell 1999; Spencer and others 2003; Minshall 2003; but see Rosenberger and others 2006 [companion paper]). One of the most obvious physical changes that may occur in streams is altered water temperature (Beschta and others 1987; Moore and others 2005a). During wildfire, intense heating can lead to short-term (<1d) increases in stream temperatures of several degrees (e.g., Hitt 2003). Over longer time frames and broader spatial scales, changes to terrestrial vegetation and stream channel morphology related to wildfire may lead to substantially altered water temperatures across stream networks, leading to loss and fragmentation of suitable habitats and increased risk of local extinction for coldwater aquatic species (Dunham and others 2003a; Pilliod and others 2003; Bury 2004; Burton 2005; Sestrich 2005).

Wildfire and associated channel disturbance may influence a number of processes that contribute to the heat budget of streams, and a large number of thermal responses are possible (Beschta and others 1987; Johnson 2003; Moore and others 2005a). Increased stream temperatures are likely following fire-related loss of shading streamside vegetation and concomitant increases in solar radiation (Brown and Krieger 1970; Dwire and Kauffman 2003). Alternatively, loss of vegetation may also cause summer base flows to increase slightly (Ziemer 1964; Jones and Post 2004), possibly leading to reduced rates of heating. However, any effects from this decrease in heating rate may by offset by an increase in the size of the low flow stream network, resulting in a longer total length of stream exposed to solar radiation. In addition, channels may be wider and more exposed to solar radiation following channel reorganizing events (Swanson 1981), but localized

changes in substrate characteristics can moderate temperatures through surface-subsurface heat exchange (Johnson and Jones 2000). Overall, it appears that habitat alterations resulting from wildfire and channel disturbance (i.e., loss of shading vegetation, channel widening) will result in a net increase in stream temperatures despite other associated habitat alterations that could reduce heating rates (i.e., increased base flow, surface-subsurface heat exchange).

In this study, we examined headwater stream temperatures in relation to wildfire and channel disturbance history in central Idaho. Our primary goal in this work was to better understand spatial and temporal changes in stream temperatures across a fire-prone landscape and to relate those changes to the distribution of sensitive species. To this end, we adopted a spatially extensive sampling design to study patterns of stream temperatures among sites within several streams with contrasting wildfire and physical disturbance histories. Previous work in other systems provided evidence for increased stream temperatures following wildfire (e.g., Minshall and others 1997), but the influence of site-specific variation (Dunham and Vinyard 1997) was not controlled among streams. To account for site variation, we compared thermal variability within and among streams in relation to wildfire and physical disturbance histories. This retrospective spatial analysis was complemented with long-term information from a fortuitous collection of samples over 3-13 years that contrasted pre-fire and post-fire temperatures in burned and unburned streams. Finally, we examined the distribution of a coldwater guild of aquatic vertebrates (salmonid fishes and amphibians) among sites and streams to determine if observed temperature changes associated with wildfire influenced patterns of species occurrence. Collectively, these results provide a broad complement of spatial and temporal perspectives on postfire patterns of stream heating and potential threats to coldwater aquatic vertebrates.

Methods

Study Area

This study was conducted in the Boise River basin, located in central Idaho (Figure 3.2.I 1). The Boise River basin is part of the Idaho batholith region, consisting of highly erodible granite rock and steep topography. Precipitation ranges from about 600-1000 mm per year, with greater amounts at higher elevations. Most precipitation falls in the winter as snow, with occasional winter or spring storms that deliver warm rains on snow that can lead to flooding. Localized flooding can also result from convective storms in summer (Miller and others 2003). Climate in the basin is typical of the region with cold, wet winters and freezing temperatures contrasting with generally hot and dry summers and air temperatures commonly exceeding 30°C.

Riparian tree species consisted primarily of willow (*Salix*, spp.), cottonwood or aspen (*Populus*, spp.), alder (*Alnus*, spp.), and birch (*Betula*, spp.). Hillslope vegetation within study streams ranges from subalpine fir (*Abies lasiocarpa*) at high elevations to mixed conifer and Ponderosa pine (*Pinus ponderosa*) forest and shrubsteppe at low elevations, with the latter becoming more prevalent on south-facing slopes. Lower elevation vegetation is characterized by mixed severity fires with return intervals of less than 35 years, whereas expected intervals for higher elevation forests may be an order of magnitude greater

(Brown and Smith 2000). Since 1992, several wildfires have burned 95,000 ha within the 217,000 ha upper Middle Fork Boise River basin upstream of Arrowrock Reservoir, a dramatic shift in fire behavior from a relatively wildfire-free period characterizing most of the 20th century. Within wildfire perimeters, burn severity was mapped by the Boise National Forest using three categories: 1) high severity – corresponding to stand-replacing fires; 2) moderate severity – corresponding to fires that burn understory vegetation with occasional burning of individual or small groups of trees; 3) low severity - corresponding to fires consuming only understory vegetation or forest litter (Figure 3.2.I 1; Burton 2005).

Stream Temperature Sampling

Pre- and post fire comparisons

We compared two fortuitous samples of stream temperatures before and after wildfires had occurred (Figure 3.2.I 1). In one case, summer (15 July-15 September) stream temperatures recorded in 1993 at two sites in different streams (Cottonwood Creek and Roaring River) were compared to each other following a wildfire in one of the streams (Cottonwood Creek) in 1994. Sampling was continued on an intermittent yearly basis through 2005. In a second case, summer (15 July to 15 September) stream temperatures recorded in 2002 at 10 sites in two streams (James and Phifer creeks) were contrasted with temperature samples taken the summer of 2004, following a severe wildfire in one of the streams in 2003 (James Creek; Figure 3.2.I 1). Water temperatures were sampled with Hobo ™ and Tidbit ™ dataloggers (Onset Computer Corporation, Pocassett, MA) before and after 2002, respectively. Field deployment of temperature dataloggers followed guidelines described in Dunham and others (2005).

Retrospective study

For a retrospective comparison of stream temperatures in relation to disturbance history, we selected streams in three major disturbance categories (Figure 3.2.I 2): 1) streams without recent stand-replacing wildfire in their watersheds; 2) streams with a recent history of moderate to high severity wildfire predominant in the watershed; 3) streams in watersheds with a recent history of moderate-high severity wildfire that were followed by massive channel reorganization from a debris flow or severe flood. Such events can occur independently of wildfire, but are much more likely after a wildfire occurs (Wondzell and King 2003). We selected streams within the three categories to contrast the effects of wildfire and fire-related channel disturbance with streams having little recent history of disturbance. Many stream catchments within the Boise River basin experienced wildfires of lesser extent or lower severity. We chose to focus on streams with relatively high degrees of potential influence to maximize detection of responses. We further restricted our analysis to headwater streams draining catchments 1000-5300 ha in area. Catchments larger than this maximum size range are influenced by wildfire, but disturbances tend to be less severe (Benda and others 1998; 2003, Miller and others 2003; C. Luce unpublished data), and large streams are less likely to experience associated changes in temperature from the loss of canopy near channels (Beschta and others 1987).

Within the range of catchment sizes and stream types (henceforth: burned, unburned, burned and reorganized), we defined stream networks and stream segments using a

geographic information system (GIS, ArcInfo Inc.) and 30 m resolution digital elevation maps (DEMs) with the TauDEM software package (Tarboton 1997; 2004). Boundaries to stream segments were identified at tributary junctions, and characteristics of the segments were estimated from DEMs, including stream channel slope (%), and contributing area (ha) and segment elevation (m) at the downstream end. These three variables are related to channel forms and landscape processes that influence stream temperatures, and thus provide a useful basis for matching streams to maximize the statistical validity of temperature comparisons among stream types (i.e., minimize confounding in statistical comparisons). We used visual inspection of scatter plots based on raw data and principal components to identify streams and segments with overlapping elevation, channel slope, and contributing areas. Within each of the three stream types, we selected three streams for sampling summer temperatures. In each of the resulting nine streams, 10 sample sites were randomly located within stream segments nested at progressively smaller catchments to a minimum of 400 ha. This design ensured that longitudinal gradients in streams were represented while maintaining randomness in the selection of specific site locations. We focused on stream segments draining catchments larger than 400 ha because in this basin they are more likely to support perennial surface flow and aquatic vertebrates. Summer stream temperatures were measured from 1 July to 15 September 2003.

Sampling of Fish and Amphibians

In the summer of 2003, we used backpack electrofishing with four removals to sample fish and amphibians in block-netted 100 m lengths of stream adjacent each site ($n = 90$) sampled for the retrospective study of stream temperature. Native vertebrates in headwater streams within the study area include rainbow trout (*Oncorhynchus mykiss*), Rocky Mountain tailed frog (*Ascaphus montanus*), and bull trout (*Salvelinus confluentus*), with localized occurrences of shorthead sculpin (*Cottus confusus*). Nonnative species include cutthroat trout (*O. clarkii*), rainbow X cutthroat trout hybrids, and brook trout (*S. fontinalis*). Focal species in this effort included the two most common native species in the Boise River basin: tailed frog and rainbow trout. Other species were recorded if found, but we considered their distributions to be too limited (e.g., bull trout, nonnative brook trout and cutthroat trout), or thermal tolerances too uncertain (e.g., shorthead sculpin) to include them in this work. A validation study conducted in 2002 (Rosenberger and Dunham 2005; Rosenberger and Dunham unpublished results) indicated this level of effort was nearly 100% effective for detecting both large (>150mm) and smaller (<150 mm) salmonid fishes. Detectability using electrofishing is unknown for adult or larval tailed frog, the only common amphibian found in our study streams. All sampling for aquatic vertebrates was conducted during base flow conditions from mid-July to mid-September. Throughout the summer, we rotated our sampling schedule for streams in each category to avoid any potential confounding of stream type and time of sampling (Appendix 3.2.I 1).

Data Analysis

Pre-post fire comparisons

For the comparison of two sites (Cottonwood Creek and Roaring River), trends in differences in postfire summer mean and maximum temperatures between the sites were assessed in relation to time since fire (year: 1995-2005) using Spearman rank correlation.

Confidence bounds for post-fire temperatures were compared to pre-fire temperature differences to determine the significance of postfire temperature changes. For the short-term (3-year) comparison of temperatures in sites sampled within James and Phifer Creeks, the significance of differences in maximum temperatures at sites in the years before and after a fire in James Creek in 2003 was assessed using *t*-tests. Paired *t*-tests were conducted to compare temperatures at sites *within* each stream (temperatures at sites sampled in 2002 versus temperatures in the same sites in 2004). An overall *t*-test was performed to compare overall average differences in temperatures before and after fire (all sites collectively) in each stream. We chose maximum temperature for this comparison because it is most likely to be responsive to changes in conditions associated with wildfire (Moore and others 2005a).

Retrospective study

To consider the probable biological implications of temperature among streams, we modeled the probability of exceeding a maximum temperature of 20°C. The biological influences of temperature vary among species, but previous work indicates occurrence of tailed frog (larvae and adults) is very unlikely when maximum temperatures approach 20°C (e.g., Pilliod and others 2003; Welsh and Lind 2002). Rainbow trout often occur at temperatures exceeding 20°C (e.g., Zoellick 1999), but temperatures of this magnitude can have adverse sublethal influences (e.g., reduced growth; Hokansen and others 1977).
To model the influence of stream type (unburned, burned, burned and channel reorganization) on biologically relevant changes in temperature, we used logistic regression to predict the probability of a site exceeding 20°C. This probability was modeled in relation to stream type and elevation, a covariate to account for longitudinal changes in stream temperature unrelated to stream type. To account for potential lack of independence in temperatures among sites sampled within streams, we used an autoregressive logistic model with an *n*-1 spatial lag (Allison 1999). We examined standard measures of model fit, including deviance statistics and Hosmer-Lemeshow goodness of fit to assess the adequacy of a logistic model (Allison 1999).
Fish and amphibian distributions

Distributions of tailed frog larvae and small rainbow trout varied little among streams, so quantitative analysis of their associations with temperature was not possible or necessary. To examine the possible influence of different timeframes, we summarized temperatures in relation to the time of sampling. This was done to allow a more precise match between observed temperatures and vertebrate distributions. These summaries included daily mean and maximum daily temperatures prior to sampling (1 July – date of sample), week prior to sampling, and day of sampling (Appendix 3.2.I 1).

Results

Pre-post Fire Comparisons

Postfire temperature data for comparing Cottonwood Creek and Roaring River were available for 1995-1997, 2001, and 2003-2005. Pre-fire summer mean and maximum temperatures were 1.1 and 1.7°C warmer in Cottonwood Creek, in comparison to Roaring

River. Following the fire in Cottonwood Creek in 1994, this temperature difference increased; mean temperatures averaged 3.7°C warmer (3.3-4.0°C, 95% CI) across sampled years following the wildfire, and maximum temperatures averaged 5.2°C (3.2-7.2°C, 95% CI) warmer. Confidence intervals for means of both temperature differences did not overlap pre-fire temperature differences, indicating statistically significant post-fire increases across the timeframe (1995-2005) sampled. The difference in mean temperature between Cottonwood Creek and Roaring River following wildfire showed a declining trend over 1995-2005, but this trend was not statistically significant (r_s=-0.66, p=0.08). The corresponding difference in maximum temperature declined more strongly and significantly, however (r_s=-0.91, p=0.002). Maximum temperature in Cottonwood Creek peaked at an unusually high level in the summer of 1996 (Figure 3.2.I 3), but inspection of temperature records did not suggest anomalies, and this observation did not influence the direction or significance of the correlation between temperature differences and time since fire.

In contrast to the comparison of pre- and post-fire temperatures at a single site over 13 years in Cottonwood Creek and Roaring River, pre- and post-fire temperature changes at multiple sites sampled in James and Phifer Creeks over three years were less obvious. Of the original 10 sites sampled within each stream, data from two sites in each stream were lost due to failure to relocate dataloggers in one year (2002 or 2004). Analyses of the eight remaining sites suggested overall average differences in maximum temperatures before and after fire were only marginally different among the two streams (t=2.06, p=0.06, df=14). Within streams, paired tests revealed significant post-fire increases in temperature in both the burned James Creek (t=-4.46, p=0.003, df=7) and unburned Phifer Creek (t=-3.38, p=0.02, df=7) creeks. Within sites in James Creek, the average pre-post fire increase in temperature was 0.9 °C (0.4, 1.4; 95% CI), whereas in Phifer Creek temperatures at sites increased an average of 0.4°C (0.1, 0.7; 95% CI).

Retrospective Study

Streams selected for the retrospective study (Figure 3.2.I 1) included three catchments with little history of recent stand-replacing fire (Beaver, Lost Man, and Trail creeks). Within these basins, stand-replacing fires were largely absent (Beaver and Lost Man creeks) or limited in area compared to wildfire that burned with lower severity (Trail Creek, Figure 3.2.I 1). Three streams selected for study with recent stand-replacing fire occurring within a major portion of their catchments included Cottonwood, Hungarian, and Lost creeks. The three selected streams with stand-replacing wildfire and recent channel reorganization (since 1992) included South Fork Sheep, Trapper, and Wren creeks. Debris flows in Trapper and Wren creeks occurred initially one year following wildfire (1995), with subsequent minor recurrences observed through 1996, whereas major channel reorganization in South Fork Sheep Creek occurred in 1993 and 1997 (J. Thornton, Boise National Forest, personal communication; C. Luce and B. Rieman, personal observations; Burton 2005). From interpretation of aerial photographs provided by the Boise National Forest, we estimated the percentage of channel reorganization (stream length) within South Fork Sheep, Trapper, and Wren creeks to be 51, 85, and 97%, respectively. Within the constraints of catchment features (e.g., area, elevation, and channel slope), spatial

proximity, and common fire histories that were present, these nine basins represented the best combination of streams we could choose for comparison in a retrospective study design.

For streams sampled as part of the retrospective study, summer maximum daily temperatures were strongly associated with stream type (unburned, burned, burned and reorganized; Appendix 3.2.I 1). Maximum daily temperatures in sites from unburned streams averaged 15.6°C, and ranged from 11.7 to 20.4°C. Maximum daily temperatures in sites from burned streams averaged 19.0°C, and ranged from 13.8 to 24.6°C. Maximum daily temperatures in sites from burned and reorganized streams were warmest, averaging 23.5°C, and ranging from 19.2 to 26.6°C. Within each stream type, the greatest range in temperatures among sites sampled within streams was associated with the largest catchments sampled (e.g., Lost Man, Cottonwood, and South Fork Sheep creeks; Figure 3.2.I 1, Appendix 3.2.I 1). Overall, 41 of the 90 sites sampled exceeded 20°C on at least one occasion during the summer of 2003.

Logistic regression indicated the probability of stream temperature exceeding 20°C was associated with both stream type (X^2 =28.9, p<0.0001, df=2) and site elevation (X^2 =3.9, p=0.05, df=1). Classification rates using a leave-one-out cross validation indicated the logistic model correctly predicted 81.1% of the observations with a classification cutoff of 0.50 for events. A plot of predicted probability of exceeding 20°C against site elevation (Figure 3.2.I 4) indicated strong differences among stream types, with sites from unburned streams showing less than 0.25 probability of exceeding 20°C, and sites from burned streams ranging from low (<0.25) to high (>0.75) probability of exceeding 20°C, and sites from burned and reorganized streams showing high (>0.75) probability of exceeding 20°C.

Fish and Amphibian Distribution

Tailed frog larvae were detected in 85 of the 90 sites sampled. Tailed frog larvae were not detected from two sites in Beaver Creek (unburned), one site in Lost Creek (burned), and one site in Wren and South Fork Sheep creeks (both burned and reorganized). Small rainbow trout occurred at every site sampled. Maximum daily stream temperatures at sites where tailed frog larvae and small rainbow trout were detected spanned the full range of observed summer temperatures (11.7-26.6°C). Examination of maximum stream temperatures prior to the dates of fish and amphibian sampling (Appendix 3.2.I 1) revealed no evidence for bias associated with matching temperatures that occurred after sampling. For example, Wren Creek was sampled after summer stream temperatures had peaked, with tailed frog larvae and small rainbow trout found in sites with maximum daily temperatures ranging from 22.5-26.6°C. This, combined with the fact that both small rainbow trout and tailed frog larvae were widespread within every stream sampled regardless of time sampled, suggested they were present in sites when summer daily maximum temperatures occurred. Finally, a plot of the catch of tailed frog larvae in relation to maximum temperatures suggested they were common (>10 individuals per site) much of the time within all sites, regardless of temperature within the observed range (Figure 3.2.I 5).

Discussion

Results of this work provide perspectives on the influences of wildfire and associated disturbances on stream temperature on both short (<5 year) and intermediate (5-11 year) timescales, including patterns from "before-after" comparisons and retrospective comparisons. Stream temperatures were strongly related to past disturbance, especially in relation to channel reorganization following wildfire. To our knowledge, there are no comparable studies of the effects of wildfire on stream temperatures at multiple sites involving these time scales. An understanding of the effects of wildfire and stream temperature at broader spatial and temporal scales is important for considering the population dynamics and local persistence of relatively mobile and longer-lived species that live in fire-prone areas, such as the stream-living vertebrates considered herein (Dunham and others 2003a; Pilliod and others 2003; Burton 2005).

Within portions of the Boise River basin, including streams sampled in the retrospective study and the pair of streams within the longer-term comparative study of stream temperatures (Figure 3.2.I 3), a consistent pattern was evident. Significantly elevated stream temperatures were apparent for at least a decade following stand-replacing wildfire. Presumably incident solar radiation was still increased over pre-fire levels in these streams (Gutiérrez-Teira and others 2006), in spite of obvious re-growth of riparian vegetation, especially deciduous species re-sprouting from roots (Dwire and Kauffman 2003). In studies of the effects of forest harvest, low-stature riparian vegetation has been found to provide some degree of shade to streams (Moore and others 2005a), but such did not appear to be sufficient to prevent elevated stream heating in our study system. Nevertheless, the fact that temperatures in burned and reorganized streams were warmest indicates that recovered streamside vegetation in burned streams does provide important shade to the stream. Longer-term increases in stream temperatures (>20 years) are more likely in systems where debris flows or severe floods completely eliminate streamside vegetation (including perennial shrubs and trees), which slows the recovery process (Gutiérrez-Teira and others 2006).

Of all components of the stream heat budget, the influence of riparian shading is the most likely mechanism for the increases in stream temperatures that we observed. However, a host of other mechanisms could also play a role (Beschta and others 1987; Johnson and Jones 2000; Moore and others 2005a). Changes in stream morphology (e.g, stream widening, loss of hyporheic exchange) following channel disturbance after wildfire could be factors that also account for the particularly high stream temperatures in these systems. In addition, pre- and post-fire differences in stream temperatures were less pronounced in the comparison of James (severely burned in 2003) and Phifer (unburned) Creeks, which lie in higher-elevation portions of the Boise River basin outside of other streams studied herein. Loss of riparian vegetation following wildfire in James Creek undoubtedly lead to increased solar insolation, but other thermal processes affecting stream temperature may have been more important, accounting for the muted response to wildfire that we observed. Among these processes, groundwater flux and hyporheic exchange may be a moderating

influence (Johnson and Jones 2000; Mellina and others 2002; Moore and others 2005b; Rothwell 2005).

Differences among streams and river basins in the prevalence of different hydrologic influences on the heat budget implies that the magnitude and duration of stream warming that we observed in the Boise River basin in burned streams may not be the case in all systems affected by wildfire. The importance of different components of the heat budget and how they are affected by wildfire in different river basins merits further study. Conceivably, it is possible through an understanding of the relative importance of different thermal processes to identify streams that may be most vulnerable to increased temperatures as a result of wildfire and channel disturbance and associated influences on stream ecosystem processes. However, the effort involved to quantify different components of the heat budgets of streams (Webb and Zhang 1997) may limit the applicability of this concept at the broad scale needed for most management applications. Accordingly, a major challenge for research is to provide a better understanding of local processes that can be efficiently transferred to understanding thermal regimes at broad scales that are most relevant for species persistence and ecosystem function (Poole and others 2004).

Biological responses we observed for rainbow trout and tailed frog larvae in relation to stream temperatures only partially met our expectations. Rainbow trout can persist within the range of temperatures observed in this study, although temperatures on the higher end of what we observed can have important sublethal effects (Li and others 1994; Zoellick 1999; Gamperl and others 2002). Accordingly, the widespread distribution or presence of rainbow was not limited by temperature. Rapid (1-year) recolonization by rainbow trout following apparent complete extirpation from channel reorganization in streams studied here (Trapper and Wren Creeks) also supports the strong resilience of rainbow trout in this system (Rieman and others 1997; Burton 2005). Studies of the responses of salmonids to comparable disturbances in other areas have shown populations to be resilient as well (Lamberti and others 1991; Roghair and others 2002; Bisson and others 2005; Sestrich 2005), unless the habitats they occupy are highly fragmented (Brown and others 2001; Dunham and others 2003). In this study, only one stream was isolated by an impassible fish movement barrier (a perched road culvert at the mouth of Lost Creek), yet the population of rainbow trout upstream persisted in the face of wildfire. However, this stream did not experience massive channel reorganization like those causing apparent extirpations of populations nearby.

In contrast to our expectations, tailed frog larvae were also distributed widely across our study streams, and occurred in nearly every site sampled, regardless of temperatures ranging up to a maximum of 26.6 °C. Most work on thermal relations of tailed frogs in the field has involved the coastal tailed frog (*Ascaphus truei*), which is generally restricted to streams with temperatures below 16°C (e.g., Hawkins and others 1988; Pilliod and others 2003; Welsh and Lind 2002). The Rocky Mountain tailed frog, recently recognized as a distinct species, has evolved separately from coastal tailed frog, likely representing isolation for more than 10 million years (Nielsen and others 2001). Published observations for this species have recorded larvae in warmer temperatures (daily maximums up to 21 °C) than would be typical for coastal tailed frog (Adams and Frissell 2001). Adams and Frissell

(2001) suggested tailed frog larvae may use cold water seeps to avoid exposure to warm temperatures. In our study streams, we found little evidence of cold water thermal refugia occurring at a site (100 m) scale, but undetected refugia could exist at much smaller scales. Alternatively, the short duration of exposure to peak daily temperatures (e.g., < 2 h) may not be sufficient to restrict the distribution of Rocky Mountain tailed frog larvae. Maximum temperatures observed in our study were less than the range of critical thermal maximums observed for coastal tailed frog larvae in the laboratory (28.9-30.1 °C; Pilliod and others 2003). Finally, it is possible that greater availability of food in warmer habitats could extend the distribution of tailed frogs. Both temperature and light are greater in streams with reduced riparian shade. Availability of food for tailed frog larvae, which graze on periphyton, may be greater in streams that receive more light (Kiffney and others 2004), potentially compensating for the physiological costs of living in warmer environments.

In conclusion, results of this work suggest several important considerations for understanding the effects of wildfire and associated influences on stream temperatures and headwater vertebrates. First, it is clear that observable changes to stream temperatures can persist for at least a decade, and likely much longer following wildfire, especially in streams experiencing channel reorganization. Second, the specific magnitude and duration of temperature changes can be difficult to predict due to uncertainties regarding the spatial and temporal variability of influences from different mechanisms influencing the heat budget of streams. This was likely reflected in the variable responses of temperature to wildfire and channel reorganization both within and among streams we studied in the Boise River Basin. Third, in spite of the sometimes dramatic physical changes to streams related to wildfire, the two vertebrate species considered herein were remarkably resilient in terms of their distribution across the landscape. Given that such disturbances have been a part of the history of streams over longer (100s-1000s of years) in this region (Kirchner and others 2001; Pierce and others 2004) it is likely these species have survived through similar, if not much larger events than studied here. Finally, in a management context, our results contribute needed empirical support for a growing consensus that management of human influences that modify species responses to wildfire (e.g., habitat degradation, fragmentation, nonnative species) may be more effective than focusing on wildfire itself as a threat to fishes and amphibians in streams (Bisson and others 2003; Bury 2004; Dunham and others 2003; Minshall 2003; Pilliod and others 2003; Rieman and Clayton 1997; Rieman and others 2003).

Acknowledgements

Funding for this work was provided by the National Fire Plan, the U.S. Forest Service Rocky Mountain Research Station, the U.S. Forest Service Regions 1 and 4, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, and local assistance from the Boise National Forest. We thank, among many, Michael Kellett, Dona Horan, Gwynne Chandler, Joseph Benjamin, Tracie Kirkham, Matt Aylsworth, Patrick Mckann, Brooke Nelson, Dan Bolin, Ciara Cusack, Tobias Jongeward, Tim Arrington, Kristin Bott, Aaron Golart, Kristen Bednarczyk, Mary Beatty, and Garet Tessmer for assistance in the field. Thanks to David Nagel, Sharon Parkes, and Joe Benjamin for support with spatial data analysis and preparation.

References 3.2.I

Adams SB, Frissell CA. 2001. Thermal habitat use and evidence of seasonal migration by Rocky Mountain Tailed Frogs, *Ascaphus montanus*, in Montana. Canadian Field-Naturalist 115: 251-256.

Allison, PD. 1999. Logistic regression using the SAS System: Theory and application. Cary, NC: SAS Institute, Inc.

Benda, L, Miller D, Dunne T, Agee J, Reeves G. 1998. Dynamic landscape systems. Naiman R, Bilby R, editors. River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. New York: Springer-Verlag New York. p261-288.

Benda L, Miller D, Bigelow P, Andras K. 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. Forest Ecology and Management 178:105-149.

Beschta, RL, Bilby RE, Brown GW, Holtby LB, Hofstra TD. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Salo EO, Cundy TW, editors. Streamside management: forestry and fishery interactions. Contribution No. 57. Washington: Institute of Forest Resources, University of Washington, Seattle. p191-232.

Bisson PA, Rieman BE, Luce C, Hessburg PF, Lee DC, Kershner JL, Reeves GH, Gresswell RE. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management 178:213-229.

Bisson, PA, Crisafulli CM, Fransen BR, Lucas RE, Hawkins CP. 2005. Responses of fish to the 1980 eruption of Mount St. Helens. Dale VH, Swanson FR, Crisafulli CM, editors. Ecological responses to the 1980 eruption of Mount St. Helens. New York: Springer-Verlag, New York. p163-182.

Brown DK, Echelle AA, Propst DL, Brooks JE, Fisher WL. 2001 Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout (*Oncorhynchus gilae*). Western North American Naturalist 61:139-148.

Brown GW, Krieger JT. 1970. Effects of clearcutting on stream temperature. Water Resources Research 4:1133-1139.

Brown JK, Smith JK. 2000. Wildland fire and ecosystems: effects of fire on flora. General Technical Report RMRS-GTR-412-vol 2, USDA Forest Service, Ogden, UT, 257p.

Burton, TA. 2005. Fish and stream habitat risks from uncharacteristic wildfire: observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. Forest Ecology and Management 211: 140-149.

Bury RB. 2004. Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests. Conservation Biology 18:968-975.

Dunham JB, Young MK, Gresswell RE, Rieman BE. 2003a. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. Forest Ecology and Management 178:183-196..

Dunham JB, Chandler G, Rieman BE, Martin D. 2005. Measuring stream temperature with digital data loggers: A user's guide. General Technical Report RMRS-GTR-150-WWW. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 15p.

Dunham JB, Vinyard GL. 1997. Incorporating stream level variability into analyses of fish-habitat relationships: some cautionary examples. Transactions of the American Fisheries Society 126:323-329.

Dwire KA, Kauffman JB. 2003. Fire and riparian ecosystems in landscapes of the western USA. Forest Ecology and Management 178:61-74.

Gamperl KA, Rodnick KJ, Faust HA, Venn EC, Bennett MT, Crawshaw LI, Keeley ER, Powell MS, Li HW. 2002. Metabolism, swimming performance, and tissue biochemistry of high desert redband trout (*Onchorynchus mykiss* ssp.): Evidence for phenotypic differences in physiological function. Physiological and Biochemical Zoology 75: 413-431.

Gresswell RE. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society 128:193-221.

Gutiérrez-Teira, B., Luce CH, Nagel D, Dunham JB. 2006. Using satellite imagery and hemispherical photography to map the effects of vegetation cover on solar radiation and stream temperatures at a basin scale. Submitted to the Journal of the American Water Resources Association.

Hawkins CP, Gottschalk LJ, Brown SS. 1988. Densities and habitat of tailed frog tadpoles in small streams near Mt. St. Helens following the 1980 eruption. Journal of the North American Benthological Society 7:246-252

Hitt NP. 2003. Immediate effects of wildfire on stream temperature. Journal of Freshwater Ecology 18:171-173.

Hokanson KEF, Kleiner CF, Thorslund TW. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:639-648.

Johnson SL. 2003. Stream temperature: scaling of observations and issues for modelling. Hydrological Processes 17:497-499.

Johnson SL, Jones JA. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 57:30-39.

Jones JA, Post DA. 2004. Seasonal and successional streamflow response to forest cutting and regrowth in the northwest and eastern United States. Water Resources Research 40:W05203, doi:10.1029/2003WR002952.

Kiffney PM, Richardson JS, Bull JP. 2004a. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. Journal of the North American Benthological Society 23:542-555.

Kirchner JW, Finkel RC, Riebe CS, Granger DE, Clayton JL, King JG, Megahan WF. 2001. Mountain erosion over 10 yr, 10 k.y., and 10 m.y. time scales. Geology 29:591–594.

Lamberti GA, Gregory SV, Ashkenas LR, Wildman RC, Moore KMA. 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences 48:196-208.

Li HW, Lamberti GA, Pearsons TN, Tait CK, Li JL, Buckhouse JC. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123:627-640.

Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19:94-100.

McMahon, TE, deCalesta DS. 1990. Effects of fire on fish and wildlife. Walstad J, editor. Natural and Prescribed Fire in Pacific Northwest Forests. Oregon: Oregon State University Press, Corvallis. p 233-250.

Mellina E, Moore RD, Hinch SG, Macdonald JS, Pearson G. 2002. Stream temperature responses to clearcut logging in British Columbia: the moderating influences of groundwater and headwater lakes. Canadian Journal of Fisheries and Aquatic Sciences 59:1886-1900.

Meyer GA, Pierce JL, Wood SH, Jull AJT. 2001. Fire, storms, and erosional events in the Idaho batholith. Hydrological Processes 15:3025-3038.

Meyer GA, Pierce JL. 2003. Climatic controls on fire-induced sediment pulses in Yellowstone National Park and central Idaho: a long-term perspective. Forest Ecology and Management 178:89-104.

Miller D, Luce C, Benda L. 2003 Time, space, and episodicity of physical disturbance in streams. Forest Ecology and Management 178:121-140.

Minshall GW. 2003. Responses of stream benthic macroinvertebrates to fire. Forest Ecology and Management 178:155-162.

Minshall GW, Robinson CT, Lawrence DE. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54:2509-2525.

Moore RD, Spittlehouse D, Story A. 2005a. Riparian microclimate and stream temperature response to forest harvesting: a review. Journal of the American Water Resources Association 41:813-834.

Moore RD, Sutherland P, Gomi T, Dhakal A. 2005b. Thermal regime of a headwater stream within a clearcut, coastal British Columbia, Canada. Hydrological Processes 19:2591-2608.

Nielson M, Lohman K, Sullivan J. 2001. Phylogeography of the tailed frog (*Ascaphus truei*): implications for the biogeography of the pacific northwest. Evolution 55:147-160.

Pierce JL, Meyer GA, Jull AJT. 2004. Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. Nature 432:87-90.

Pilliod DS, Bury RB, Hyde EJ, Pearl CA, Corn PS. 2003. Fire and amphibians in North America. Forest Ecology and Management 178:163-182.

Poole GC, Dunham JB, Keenan DM, Sauter ST, McCullough DA, Mebane C, Lockwood JC, Essig DA, Hicks MP, Sturdevant DJ, Materna EJ, Spalding SA, Risley J, Deppman M. 2004. The case for regime-based water quality standards. BioScience 54:154-161.

Rieman BE, Clayton J. 1997. Wildfire and native fish: issues of forest health and conservation of native fishes. Fisheries. 22:6-15.

Rieman, BE, Lee DC, Chandler G, Myers D. 1997. Does wildfire threaten extinction for salmonids: responses of redband trout and bull trout following recent large fires on the Boise National Forest. Greenlee J, editor. Proceedings of the Conference on Wildfire and Threatened and Endangered Species and Habitats, November 13-15, 1995, Coeur d'Alene Idaho. Washington: International Association of Wildland Fire, Fairfield. p47-57.

Roghair CN, Dolloff CA, Underwood MK. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Transactions of the American Fisheries Society 131:718-730.

Rosenberger AE, Dunham JB. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395–1410.

Rosenberger AE, Dunham JB, Wipfli MS, Buffington JM. 2006. Effects of wildfire and channel reorganization on drifting macroinvertebrates and predation by trout in central Idaho streams a decade after disturbance. Submitted to *Ecosystems* as a companion paper to this manuscript.

Rothwell EL. 2005. The influence of hyporheic flow on the temperature of a riffle-step-pool stream. Thesis (M.S.), Boise State University, 2005. 88p.

Sestrich CM. 2005. Changes in native and nonnative fish assemblages and habitat following wildfire in the Bitterroot River Basin, Montana. Thesis (M.S.), Montana State University. 93p.

Spencer CN, Gabel KO, Hauer FR. 2003. Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. Forest Ecology and Management 178:141-153.

Swanson FJ. 1981. Fire and geomorphic processes. Mooney HA, Bonnicksen TM, Christensen NL, Lotan JE, Reiners WA, editors. Fire regimes and ecosystem properties: USDA Forest Service General Technical Report WO-26, Washington D.C.

Tarboton DG. 1997. A new method for the determination of flow directions and contributing areas in grid digital elevation models. Water Resources Research 33:309-319.

Tarboton DG. 2004. Terrain Analysis Using Digital Elevation Models: a graphical user interface software package for the analysis of digital elevation data and mapping of channel networks and watersheds. Utah Sate University, Logan, UT.

Webb BW, Zhang Y. 1997. Spatial and seasonal variability in the components of the river heat budget. Hydrological Processes 11:79-101.

Welsh HH, Lind AJ. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou region of California and Oregon. Journal of Wildlife Management 66:581-602.

Wondzell SM, King JG. 2003. Postfire erosional processes in the Pacific Northwest and Rocky Mountain regions. Forest Ecology and Management 178:75-88.

Ziemer RR. 1964. Summer evapotranspiration trends as related to time after logging of forests in Sierra Nevada. Journal of Geophysical Research 69:615-620.

Zoellick BW. 1999. Stream temperatures and the elevational distribution of redband trout in southwestern Idaho. Great Basin Naturalist 59:136–143.

Figure Legends (3.2.I)

Figure 3.2.I 1. Shaded elevation map of Boise River basin indicating blue stream lines and sites sampled for stream temperatures and vertebrates in nine streams during the summer of 2003 (closed circles), sites sampled for stream temperatures for summers of 1993-2005 (Cottonwood Creek and Roaring River; open circles), and sites sampled for stream temperatures for the summers of 2002 and 2004 (James and Phifer Creeks; open stars). Wildfires occurring in different years are indicated by outlines around fire perimeters (black outline = 1992; white line = 1994; green line = 2000; purple line = 2003). Colors within fire perimeters indicate the severity of wildfires determined by the Boise National Forest, with darkest red corresponding to high severity wildfire, light pink corresponding to low severity wildfire, and an intermediate shade of red corresponding to moderate severity wildfire. Note the spatial resolution of fire severity mapping was greater in 2000 and 2003.

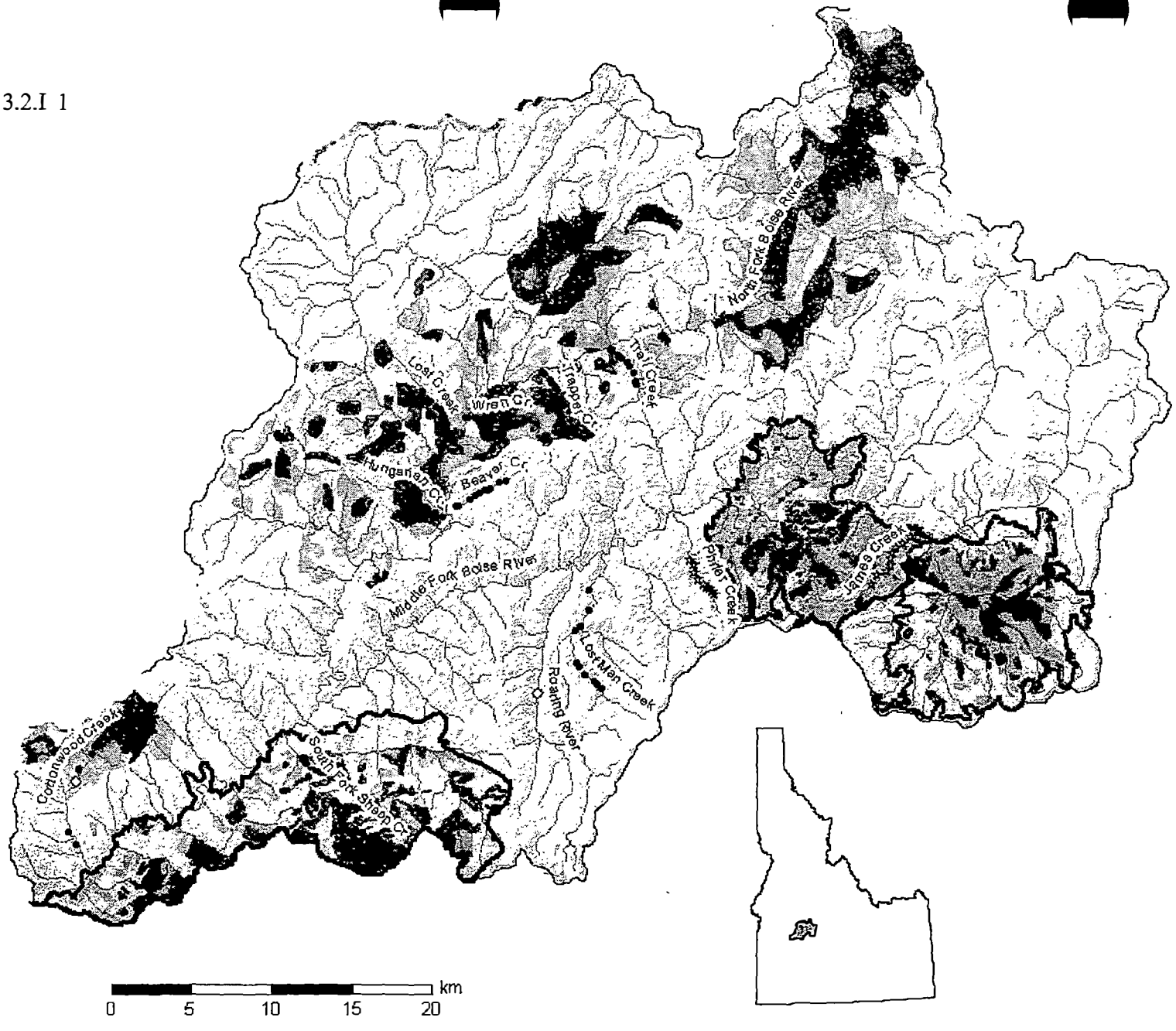
Figure 3.2.I 2. Photographs of sampling sites taken during the summer of 2003 for three different headwater stream types as relates to wildfire and channel disturbance history. A) streams without recent stand-replacing wildfire in their watersheds; B) streams with moderate –high severity wildfire predominant in the watershed; C) streams with moderate-high severity wildfire that resulted in massive channel reorganization. Wildfire and channel disturbance took place in pictured sites 1994 and 1995, respectively.

Figure 3.2.I 3. The difference between mean (unfilled symbols) and maximum (filled symbols) summer stream temperatures of two streams recorded across 13 years in the Boise River basin (Figure 3.2.I 1) with differing burn histories. Timing of the wildfire in Cottonwood Creek is indicated by the vertical dotted line (1994). Temperature differences were calculated by subtracting temperatures recorded in Cottonwood Creek (burned) from those recorded in Roaring River (unburned).

Figure 3.2.I 4. Plot of predicted probability of exceeding 20°C as a function of stream elevation for sites in nine stream in the Boise River basin (Figure 3.2.I 1) with differing wildfire and channel disturbance history (closed circles = unburned streams; open circles = burned streams; gray triangles = burned and reorganized streams).

Figure 3.2.I 5. Plot of the total catch of tailed frog for each site sampled (n=90) against maximum summer temperature of the site in streams in the Boise River basin with differing burn histories (closed circles = unburned streams; open circles = burned streams; gray triangles = burned and reorganized streams)

Figure 3.2.I 1


North Fork Boise River
Trail Creek
Lost Creek
Wren Cr.
Trapper Cr.
Hungarian Cr.
Beaver Cr.
Middle Fork Boise River
Phifer Creek
James Creek
Lost Man Creek
Roaring River
Cottonwood Creek
South Fork Sheep Cr.
km
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5
10
15
20

Figure 3.2.I 2A

Figure 3.2.I 2B

Figure 3.2.1 2C

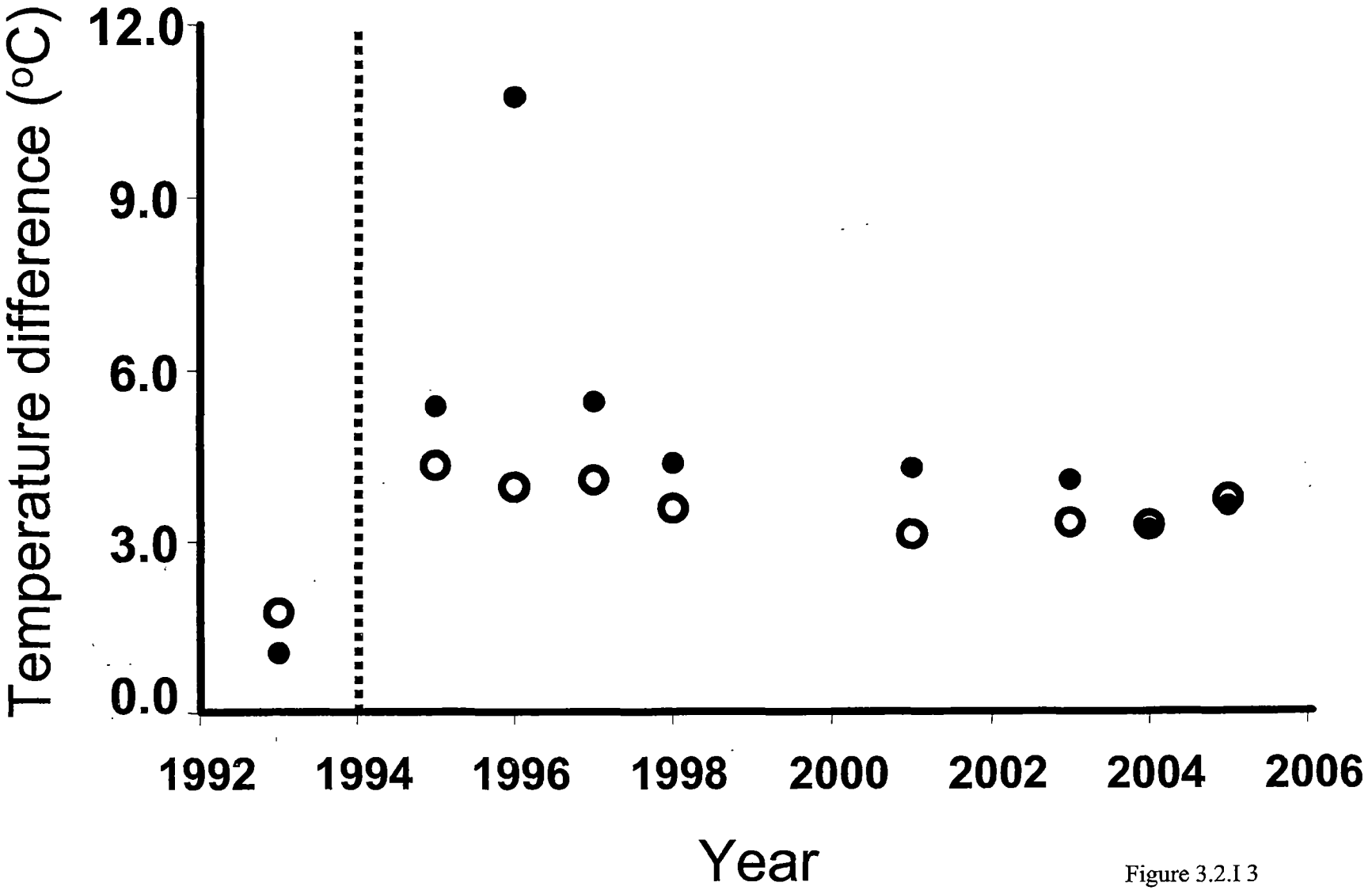

Temperature difference (°C)
12.0
9.0
6.0
3.0
0.0
1992
1994
1996
1998
2000
2002
2004
2006
Year

Figure 3.2.I 3

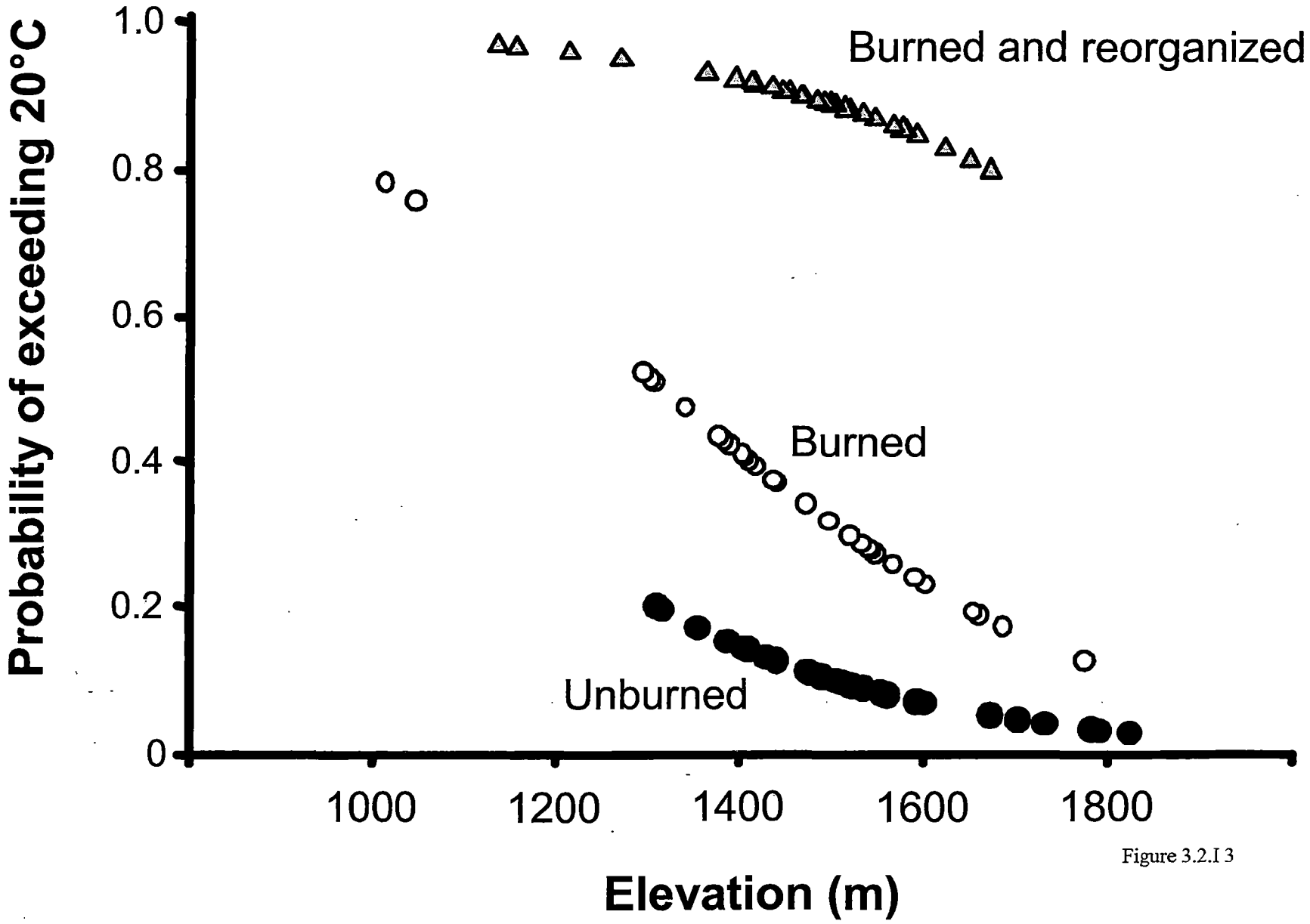

Probability of exceeding 20°C
1.0
0.8
0.6
0.4
0.2
0
Burned and reorganized
Burned
Unburned
1000
1200
1400
1600
1800
Elevation (m)

Figure 3.2.I 3

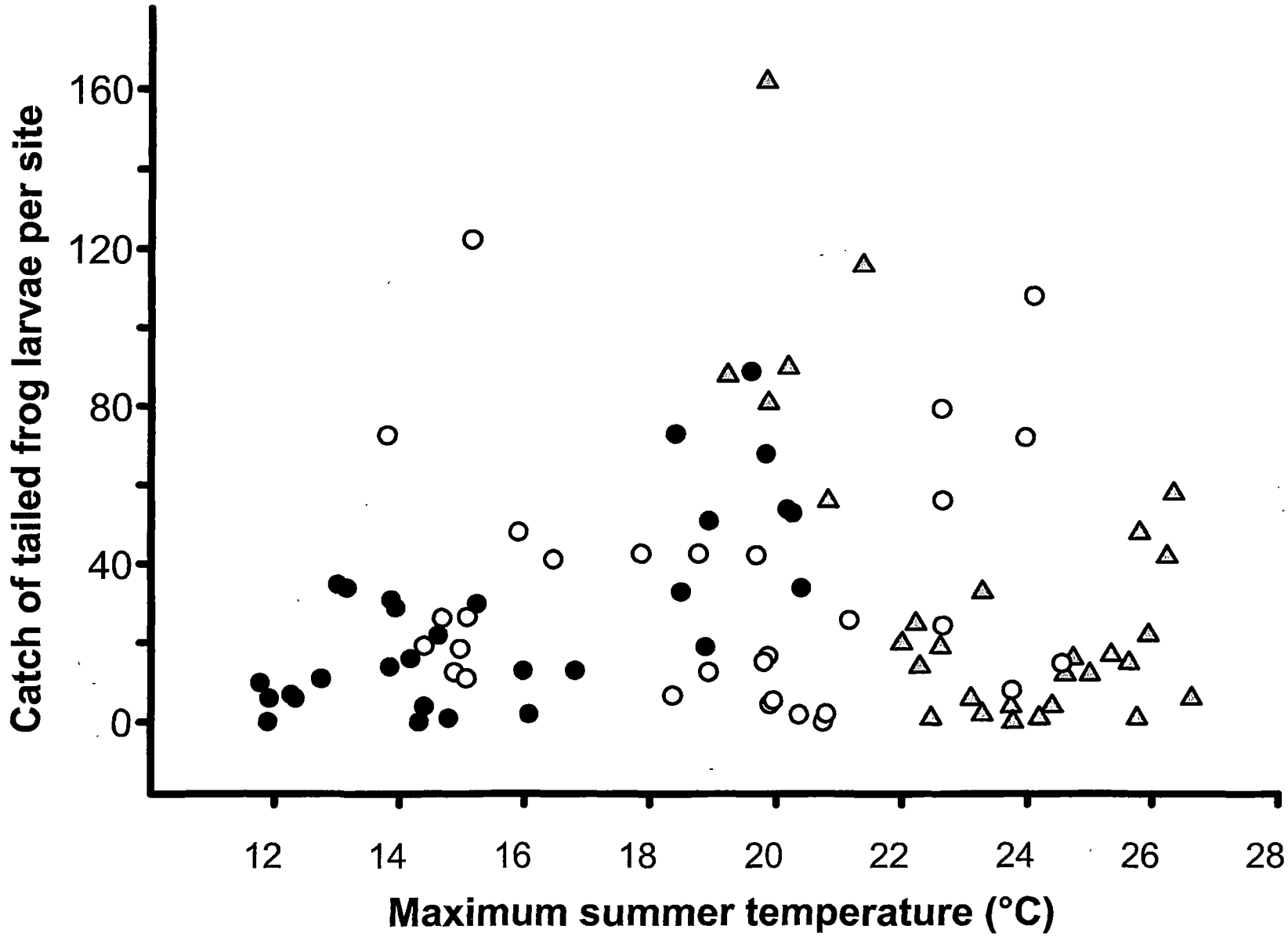

Catch of tailed frog larvae per site
160
120
80
40
0
12
14
16
18
20
22
24
26
28
Maximum summer temperature (°C)

Figure 3.2.I 4

Appendix 3.2.I 1. Summer maximum temperatures by disturbance history (UB = unburned; BR = burned; RB = burned and reorganized), stream, and site and different temporal windows, including the time the site was sampled for vertebrates (*** = missing data).

Stream name	Stream type	Site elevation (m)	Julian day of vertebrate sampling	Maximum temperature on sampling day	Maximum temperature on sampling week	Maximum temperature from July 1 to sampling day	Summer daily maximum temperature	Julian day of summer maximum temperature	Summer daily maximum minus maximum temperature on sampling day	Summer daily mean temperature
Beaver	UB	1510	227	14.0	14.0	14.9	14.8	201	0.8	11.3
Beaver	UB	1479	226	12.1	12.1	14.3	14.3	209	2.2	10.4
Beaver	UB	1439	228	11.6	11.7	11.9	11.9	201	0.3	9.7
Beaver	UB	1429	225	12.0	12.3	12.3	12.3	201	0.3	9.8
Beaver	UB	1429	210	11.8	11.8	11.9	11.9	201	0.2	9.6
Beaver	UB	1409	211	12.3	12.3	12.3	12.3	210	0.0	9.7
Beaver	UB	1386	208	12.2	12.9	12.9	13.2	210	0.9	10.0
Beaver	UB	1355	207	11.7	13.7	13.7	13.9	212	2.2	10.6
Beaver	UB	1315	198	12.3	13.4	13.4	14.2	201	1.9	10.5
Beaver	UB	1309	196	13.2	13.5	13.5	14.4	201	1.2	10.7
Lost Man	UB	1823	253	6.8	10.2	11.8	11.8	201	4.9	9.3
Lost Man	UB	1790	258	6.6	9.3	12.8	12.8	201	6.2	9.7
Lost Man	UB	1782	254	7.9	10.8	13.0	13.0	201	5.1	9.9
Lost Man	UB	1731	259	7.3	8.4	14.6	14.6	227	7.3	10.5
Lost Man	UB	1702	260	5.9	8.6	13.8	13.8	203	7.9	10.5
Lost Man	UB	1671	265	6.8	7.6	13.9	13.9	201	7.1	10.7
Lost Man	UB	1590	266	8.0	8.6	16.1	16.1	202	8.1	11.5
Lost Man	UB	1553	267	7.5	7.9	16.8	16.8	201	9.4	11.9
Lost Man	UB	1512	273	11.6	11.6	18.9	18.9	202	7.2	12.4
Lost Man	UB	1404	274	10.0	11.0	18.7	18.7	201	8.6	13.1

Trail	UB	1599	230	13.0	14.0	15.2	15.2	201	2.2	11.1
Trail	UB	1593	231	14.4	14.9	16.0	16.0	201	1.6	11.4
Trail	UB	1561	225	16.7	16.7	18.5	18.5	201	1.8	12.6
Trail	UB	1559	225	16.8	16.8	18.4	18.4	201	1.6	12.6
Trail	UB	1534	224	15.7	16.8	18.9	18.9	201	3.2	12.8
Trail	UB	1522	222	17.2	17.5	19.6	19.6	201	2.4	13.0
Trail	UB	1502	221	17.3	17.6	19.8	19.8	201	2.6	13.2
Trail	UB	1489	215	15.2	19.3	20.2	20.2	201	5.0	13.3
Trail	UB	1475	214	14.6	19.7	20.4	20.4	201	5.8	13.5
Trail	UB	1473	213	18.8	19.6	20.3	20.3	201	1.5	13.5
Cottonwood	BR	1774	210	17.5	17.7	17.7	17.9	211	0.3	12.3
Cottonwood	BR	1685	211	18.7	19.7	19.7	19.7	204	1.0	13.0
Cottonwood	BR	1601	210	21.6	22.6	22.6	22.6	204	1.0	14.8
Cottonwood	BR	1542	204	23.9	24.1	24.1	24.1	201	0.2	17.0
Cottonwood	BR	1406	203	24.0	24.0	24.0	24.0	201	0.0	16.7
Cottonwood	BR	1307	198	19.7	21.0	21.0	22.6	201	3.0	16.3
Cottonwood	BR	1303	197	21.0	21.0	21.0	22.6	201	1.7	16.4
Cottonwood	BR	1047	196	22.2	22.5	22.5	24.6	201	2.4	16.7
Cottonwood	BR	1653	210	20.2	21.1	21.1	21.1	204	1.0	13.8
Cottonwood	BR	1013	195	21.3	21.7	21.7	23.8	201	2.5	17.0
Hungarian	BR	1471	233	10.8	13.3	13.8	13.8	201	3.0	10.6
Hungarian	BR	1437	231	13.3	13.8	14.4	14.4	201	1.1	10.9
Hungarian	BR	1418	234	12.4	13.9	14.7	14.7	201	2.3	11.1
Hungarian	BR	1411	238	12.5	14.2	15.0	15.0	201	2.5	11.3
Hungarian	BR	1402	239	13.2	14.2	14.9	14.9	201	1.7	11.1
Hungarian	BR	1389	246	12.9	13.3	15.0	15.0	201	2.2	11.2
Hungarian	BR	1383	240	13.2	13.3	15.0	15.0	201	1.9	11.3
Hungarian	BR	1377	247	13.3	13.3	15.1	15.1	201	1.9	11.3
Hungarian	BR	1340	254	10.3	13.5	15.9	15.9	201	5.6	11.7
Hungarian	BR	1294	252	9.3	13.6	16.4	16.4	201	7.2	12.1
Lost	BR	1565	250	14.5	16.0	19.9	19.9	201	5.4	14.0
Lost	BR	1659	253	***	14.0	18.3	18.3	201	18.3	12.6
Lost	BR	1589	252	10.7	16.8	20.8	20.8	201	10.1	14.4

Lost	BR	1547	250	14.6	16.2	20.4	20.4	201	5.8	14.1
Lost	BR	1539	248	15.5	16.5	20.8	20.8	201	5.3	14.2
Lost	BR	1532	270	***	***	19.9	19.9	201	19.9	14.0
Lost	BR	1532	239	16.0	17.6	19.8	19.8	201	3.9	14.2
Lost	BR	1519	238	14.4	16.4	18.8	18.8	201	4.5	14.1
Lost	BR	1497	233	13.9	17.6	18.9	18.9	201	5.1	14.3
Lost	BR	1441	232	18.3	18.6	19.9	19.9	201	1.6	14.7
SF Sheep	RB	1672	239	15.7	17.0	19.2	19.2	201	3.5	12.0
SF Sheep	RB	1649	238	15.2	17.6	19.8	19.8	201	4.6	12.4
SF Sheep	RB	1567	240	15.9	16.7	20.2	20.2	201	4.3	13.1
SF Sheep	RB	1504	247	***	16.2	19.9	19.9	201	19.9	13.7
SF Sheep	RB	1453	231	18.4	18.9	20.8	20.8	201	2.4	13.9
SF Sheep	RB	1415	226	18.8	18.8	21.4	21.4	201	2.6	14.4
SF Sheep	RB	1271	225	19.1	19.7	22.0	22.0	201	2.9	15.2
SF Sheep	RB	1215	224	19.3	20.3	22.3	22.3	201	2.9	15.9
SF Sheep	RB	1156	219	21.1	22.7	23.7	23.7	201	2.7	16.4
SF Sheep	RB	1138	217	22.1	23.2	23.8	23.8	201	1.7	16.6
Trapper	RB	1622	211	21.9	21.9	22.2	22.2	203	0.3	14.9
Trapper	RB	1593	211	22.3	22.3	22.6	22.6	201	0.3	15.1
Trapper	RB	1579	210	22.9	23.3	23.3	23.3	206	0.3	15.4
Trapper	RB	1548	210	24.5	25.0	25.0	25.0	201	0.5	16.1
Trapper	RB	1534	204	23.6	24.6	24.6	24.6	201	1.0	16.1
Trapper	RB	1493	203	25.3	25.6	25.6	25.6	201	0.4	16.6
Trapper	RB	1470	202	25.6	25.9	25.9	25.9	201	0.4	16.7
Trapper	RB	1455	197	23.7	24.1	24.1	25.8	201	2.1	16.7
Trapper	RB	1436	196	23.3	24.5	24.5	26.2	201	2.9	16.8
Trapper	RB	1417	195	24.1	24.8	24.8	26.3	201	2.3	17.0
Wren	RB	1576	267	15.5	16.0	26.6	26.6	201	11.1	18.0
Wren	RB	1519	267	14.8	15.4	24.7	24.7	201	10.0	17.3
Wren	RB	1515	266	15.3	15.7	25.3	25.3	201	10.0	17.3
Wren	RB	1499	266	16.2	16.3	25.8	25.8	201	9.6	17.4
Wren	RB	1484	265	14.6	14.6	24.2	24.2	201	9.6	16.7
Wren	RB	1467	261	12.2	15.8	23.3	23.3	201	11.1	16.5

Wren	RB	1455	260	11.4	15.2	23.1	23.1	201	11.7	16.7
Wren	RB	1448	260	11.3	14.9	22.5	22.5	201	11.1	16.8
Wren	RB	1396	259	13.1	16.4	23.8	23.8	203	10.6	17.4
Wren	RB	1363	253	14.5	19.4	24.4	24.4	201	9.9	17.8

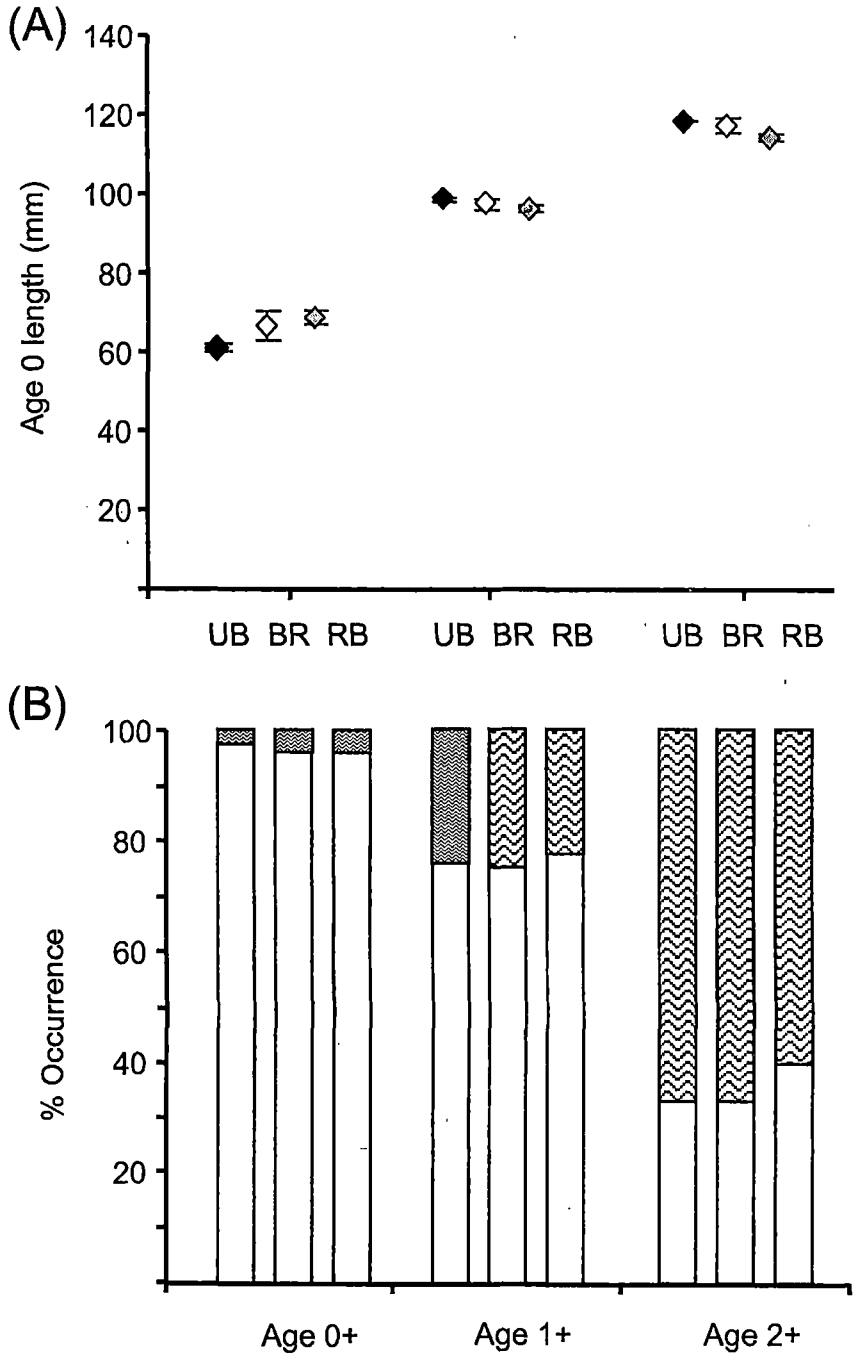


Figure 3.2.III 6

RESEARCH AREA 3 * GOAL 2 * PUBLICATION II

Effects of wildfire and channel reorganization on drifting macroinvertebrates and trout diet in central Idaho streams a decade after disturbance

Abstract.- In this study, we examined the relationship between wildfire and subsequent channel reorganization (postfire debris flows and floods) on the food base of rainbow trout (*Oncorhynchus mykiss*, Walbaum) in Idaho headwater streams 9–11 years after disturbance. Although wildfire is recognized as an important ecological driver in western stream ecosystems, we have limited understanding of its influences on ecological processes for intermediate time scales (10–100 years). In streams with different disturbance histories (unburned, burned, burned with channel reorganization), we examined characteristics of aquatic macroinvertebrate drift and rainbow trout diet for summer and autumn sampling periods. We related observed differences to stream features that have potential to affect the macroinvertebrate community (overhead cover, water temperature, and substrate diversity and mobility), which may be affected by wildfire and channel reorganization. Macroinvertebrate prey densities were more variable within disturbance types than among them and did not show a relationship with measured habitat features. More subtle features of macroinvertebrate drift, average body size and taxonomic richness, were primarily related to water temperature, and secondarily influenced by disturbance history. There were also differences among disturbance types in the amount of terrestrial insects in rainbow trout diets during autumn, which may be related to the amount and type of overhead canopy available. Taxonomic richness was unrelated to both substrate diversity and mobility, despite the observation that mobility was slightly lower in burned and reorganized streams. Results of this work suggest there are detectable, but subtle, changes to drifting prey in response to direct and indirect effects of wildfire over intermediate time scales. We emphasize the importance of relating underlying physical conditions, rather than broad treatment classifications, to observed biotic patterns for understanding ecosystem response.

Introduction

Natural disturbances such as wildfire play a key role in aquatic ecosystems (Gresswell, 1999). Effects of wildfire on headwater streams in montane landscapes may be particularly important because they are strongly influenced by riparian vegetation (Dwire & Kauffman, 2003) and sediment transport from adjacent hillslopes and steep tributaries (Benda *et al.,* 1998; 2003; Montgomery, 1999). Wildfire can alter basin hydrology and hillslope erosional thresholds, increasing the probability of severe erosional events (floods; debris and hyperconcentrated flows) that can result in loss of riparian vegetation, channel reorganization (massive change due to widespread aggradation, scour to bedrock or extensive removal/addition of wood debris), and local extirpation of aquatic species (e.g., Pilliod *et al.,* 2003). However, periodic disturbances such as wildfire may play an important long-term role in stream ecosystem function (Reeves *et al.,* 1995; Lytle & Poff, 2004).

Studies of how wildfire affects stream ecosystem function rarely extend beyond immediate impacts (but see Minshall, Royer, & Robinson, 2001), perhaps because effects are most obvious 0–10 years after disturbance (Minshall, Brock, & Varley, 1989; Minshall, 2003). On timescales of hundreds to thousands of years, wildfire effects are understood within a context of fire regimes driven by broad changes in climate and vegetation (Meyer, Wells, & Jull 1995; Pierce, Meyer, & Jull 2004). At intermediate time scales (>10–100 years; Fausch *et al.,* 2002), effects of wildfire are the least understood, but perhaps most relevant for designing management strategies for aquatic ecosystems (Bisson *et al.,* 2003).

Alterations in stream habitat associated with wildfire and subsequent channel reorganization that persist over intermediate time scales have the potential to affect multiple components of stream ecosystem function. In this study, we examined the relationship between wildfire and subsequent channel reorganization on the food base of rainbow trout (*Oncorhynchus mykiss*, Walbaum) 9-11 years after wildfire. We related observed differences to stream habitat features that may vary with disturbance history. We hypothesized that three potential influences of wildfire on stream habitat could affect macroinvertebrate prey and predation by rainbow trout: reductions in riparian vegetation, increases in stream temperature, and alteration of substrate diversity and mobility.

Wildfire-related reductions in streamside vegetation could affect drifting macroinvertebrates in a variety of ways. The amount of terrestrial macroinvertebrates falling into streams —an important energy source for trout (Kawaguchi, Yoshinori, & Nakano, 2003)— has been positively associated with riparian vegetation cover (Wipfli, 1997; Kawaguchi & Nakano, 2001). Loss of riparian vegetation due to wildfire could also reduce the amount of allochthonous energy sources available for aquatic macroinvertebrates (e.g., terrestrial plant material; Cummins *et al.,* 1989), while reduced shading could lead to an increase in available autochthonous energy sources (e.g., algae; Fuller, Kennedy, & Nielsen, 2004; Li *et al.,* 1994; Hill, Ryon, & Schilling, 1995). However, streamside areas often experience low fire severity and recover rapidly (Camp *et al.,* 1997; Taylor & Skinner, 1998; Dwire & Kauffman, 2003). In such cases, aquatic macroinvertebrates may benefit from the combined allochthonous energy inputs of streamside deciduous vegetation that recovers rapidly after fire (e.g., willows [*Salix* spp.], alders [*Alnus* spp.]), together with increased solar radiation resulting from the loss of more slowly recovering forest trees (e.g., Douglas fir [*Pseudotsuga menziesii*]; Mihuc & Minshall, 1995; but see Perry, Bradford, & Grout, 2003). In contrast, channel reorganization following wildfire can reset successional dynamics of streamside vegetation and slow riparian recovery (Dwire & Kauffman, 2003; C. Luce, unpubl. data), potentially prolonging the dependence of aquatic macroinvertebrates on autochthonous energy sources (Mihuc & Minshall, 1995).

Increased solar radiation entering streams after wildfire may also affect the macroinvertebrate prey base by increasing stream temperatures (Beschta *et al.,* 1987; Minshall, Brock, & Varley, 1989; Dunham *et al., in press*). The effects of stream warming on aquatic macroinvertebrates may be such that some taxa disappear entirely from streams, either through wholesale loss of intolerant species (Vannote & Sweeney, 1980) or earlier onset of adult insect emergence (Hogg & Williams, 1996; Frutiger & Imhof, 1997). For other taxa, individual growth may be stunted if metabolism increases with temperature at a rate disproportionate to assimilation (Vannote & Sweeney, 1980). Consequently, macroinvertebrate populations subjected to warming temperatures have been characterized by lower densities, smaller individuals, and fewer taxa (Vannote & Sweeney, 1980; Hogg & Williams, 1996), all of which could affect aquatic predators.

In streams affected by wildfire, postfire channel reorganization may alter the spatial distribution of substrate textural patches (Buffington & Montgomery, 1999a) and the diversity of substrate sizes. Diversity in substrate sizes generally varies positively with aquatic macroinvertebrate taxonomic richness (Culp, Walde, & Davies, 1983; Reice, Wissmar, & Naiman, 1990; Brown, 2003). In addition, changes in stream flow depth and channel slope after channel reorganization may alter boundary shear stress and substrate mobility. Although the effects of substrate disturbance on macroinvertebrates are inconsistent (Reice, Wissmar, & Naiman, 1990; Matthaei, Uehlinger, & Frutiger, 1997; Death, 2003), low-intensity disturbances brought about by frequent substrate mobility could increase aquatic macroinvertebrate taxonomic richness (McCabe & Gotelli, 2000).

By examining how the prey base for rainbow trout changes in response to wildfire and habitat features influenced by wildfire over intermediate time scales, we hope to gain insight into broader questions about how natural disturbances influence stream ecosystem function (Resh *et al.,* 1988; Wootton, Parker, & Power, 1996). An understanding of how specific types of disturbance and consequent changes in physical and biological conditions affect stream ecosystems is needed to provide a context for land management in the face of increasing human influences on both individual species and ecosystem conditions in fire-prone regions (Bisson *et al.*, 2003). These types of disturbance may become increasingly common as climate change increases the frequency and extent of wildfire in the western United States (Westerling *et al.,* 2006).

Methods

Study Area and Experimental Design

This work was conducted in tributaries of the Middle and North forks of the Boise River (Boise National Forest, central Idaho) in the Idaho batholith region. Several wildfires have burned 95,000 ha within the 217,000 ha upper Middle Fork Boise River Basin upstream of Arrowrock Reservoir since 1992. Within wildfire perimeters, burn severity was mapped by the Boise National Forest using three categories: 1) high severity – corresponding to stand-replacing fires; 2) moderate severity – corresponding to fires that burn understory vegetation with occasional burning of individual or small groups of trees; and 3) low severity - corresponding to fires consuming only understory vegetation or forest litter (Figure 3.2.II 1; Burton, 2005). The streams sampled for this study were influenced by stand-replacing wildfires occurring in 1992 and 1994 (Figure 3.2.II 1).

Characteristics of macroinvertebrate drift and diets of rainbow trout were determined for 9 streams, 3 in each of the following disturbance categories: unburned, burned, and burned and reorganized. According to records maintained by the Boise National Forest, unburned streams had not experienced wildfire in nearly a century (Lost Man and Beaver creeks) or were only lightly burned (Trail Creek). Burned streams experienced stand-replacing fires throughout most of their catchments (Cottonwood,

Hungarian, and Lost creeks). We focused on stand-replacing wildfires to maximize our chances of detecting differences among stream types. In burned and reorganized streams (South Fork Sheep, Trapper, and Wren creeks), stand-replacing wildfires were followed by small, isolated thunderstorms that triggered massive channel-reorganizing debris flows and hyperconcentrated floods (Benda *et al.*, 2003). Although such events can occur in wildfire-free watersheds, they are more likely to occur after severe wildfire (Wondzell & King, 2003). We sampled aquatic macroinvertebrate drift and rainbow trout diets in mid-summer and autumn to capture differences between seasons and to cover the critical period for rainbow trout feeding before winter.

Field Sampling of Drift and Fish Diets

Wesampled aquatic macroinvertebrate drift in summer (July 21–25) and autumn (October 4–7) of 2003 following procedures described by Wipfli & Gregovich (2002). Drift nets were placed and secured with sandbags in swift water areas at habitat unit breaks (riffle/cascade breaks) such that they included surface water. A portion of the stream flow was diverted through a polyvinyl chloride (PVC) pipe (1-m long, 10-cm inside diameter), and drift nets (10-cm-diameter mouth, 2 m long, 250-μm mesh) were attached to the outflow end of each pipe (Wipfli & Gregovich, 2002). Drift nets captured aquatic macroinvertebrates continuously for a 48 h period for each sampling occasion (nets were checked after 24 h for clogging). Discharge from the pipe was measured by using a stopwatch to count the number of seconds it took for water from the outflow pipe to fill a container of known volume at the beginning and end of the sampling period and averaged. Changes in flow through drift nets over the sampling period were negligible. Contents of the drift nets, including detritus and macroinvertebrates, were collected and preserved in 95% ethanol. Terrestrial as well as aquatic macroinvertebrates were captured using this technique; however, differences in surface water entering the nets and differences between the vulnerability of terrestrial insects that accidentally fall into the water column and aquatic insects to fish predation had potential to bias comparisons; therefore, we limited our analysis of drift to aquatic macroinvertebrates, including adults of aquatic origin.

With the exception of Cottonwood Creek, drift sampling locations were 300 m upstream from the confluence of the tributary with the Middle Fork or North Fork of the Boise River. A significant length of stream upstream of the mouth of Cottonwood Creek was unburned or only lightly burned (Figure 3.2.II 1); therefore, we sampled approximately 300 m upstream of the downstream extent of the severe burn in this system. For diet analysis, rainbow trout > 60 mm were collected upstream of the drift net sampling locations (between 1 km to 4 km stream length) within 2 wk following drift sampling (August 4–12 and October 7–8, 2003; Table 3.2.II 2). Fish were captured during daylight hours between 11AM and 6PM. Sampling was staggered among disturbance types to avoid bias associated with diel patterns of fish feeding. Fish stomach contents were sampled using a gastric lavage or by sacrificial sampling. A subset of fish sampled using a gastric lavage were sacrificed to ensure that the lavage adequately evacuated fish stomach contents.

Field Sample Processing

To economize effort, macroinvertebrates in drift samples with large numbers of individuals (> 500) were randomly subsampled during processing using a Caton subsampling tray (Caton, 1991; percent processed during summer and fall, respectively: Beaver Creek 100, 38; Cottonwood Creek 30, 100; Hungarian Creek 73, 70; Lost Creek 100, 100; Lost Man Creek 40, 75; South Fork Sheep Creek 23, 62; Trail Creek, 15; 62; Trapper Creek 37, 75; Wren Creek 37; 100). The Caton tray contained a grid of 30 equal-sized squares. Subsamples were sequentially selected from randomly chosen squares until 500 individuals were counted. The macroinvertebrates were sorted under a dissecting scope, identified to the lowest reliable taxon (most identified at least to family), measured to the nearest millimeter

(length excluding antennae and cerci), and enumerated. Sizes of partially digested prey items were estimated from intact individuals of the same taxon of similar size. Individual biomass (mg dry mass) was estimated using published taxon-specific length-weight regression equations (Rogers, Buschbom, & Watson, 1977; Smock, 1980; Sample *et al.,* 1993; Burgherr & Meyer, 1997).

The following variables were used to describe sampled aquatic macroinvertebrate drift for each stream: (1) aquatic macroinvertebrate drift biomass density (mg dry mass per m^3 of water), (2) average body size of individual macroinvertebrates (mg dry mass), and (3) taxonomic richness standardized using a rarefaction technique. Different numbers of macroinvertebrates processed for each sample could bias taxonomic richness measures (Gotelli & Colwell, 2001); as more individuals are processed and observed, more taxa are recorded (Bunge & Fitzpatrick, 1993). We avoided this pitfall using a rarefaction technique to standardize our taxonomic richness measurements (standard *n*: summer = 110, autumn = 180). This technique is outlined in Gotelli & Colwell (2001) and is easily performed using the readily available program EcoSim (© 1997–2004, Acquired Intelligence Inc., http://www.garyentsminger.com/ecosim/index.htm).

Stomach content data for individual trout were combined for each stream, and the following variables used to describe rainbow trout stomach contents: (1) % biomass of terrestrial origin (mg dry mass), (2) taxonomic richness of aquatic macroinvertebrates, and (3) average body size of aquatic macroinvertebrates (mg dry mass). As described previously, we used rarefaction to standardize measurements of taxonomic richness (standard *n*, summer and autumn = 85).

Habitat Measurements

Vegetation cover characteristics in each stream were quantified from 30 m resolution LANDSAT 7 ETM+ thematic mapper satellite imagery acquired on July 10, 2002 (C. Luce & D. Nagel, Boise Aquatic Sciences Laboratory, unpubl. data). Vegetation type measurements using this technique correlated strongly with ground-based measures of solar radiation and therefore provide useful surrogates for riparian vegetation cover (Luce, unpubl. data). The cover measurement used was the proportion of stream length with open canopy for a 1 km reach upstream of the drift sampling locations.

Summer temperatures at each site were recorded by temperature loggers (Onset® tidbits, Onset Computer, Pocasset, MA) deployed within 1 stream km of the drift sampling locations. Field deployment of temperature loggers followed Dunham *et al.,* (2005). Temperature loggers were programmed to record stream temperatures every 30 minutes from July 1 to September 2, 2003, a period which includes the warmest days of the year (Dunham *et al., in press*). Maximum summer temperature strongly correlates with other measures of stream temperature (e.g., median or mean temperatures; Dunham *et al.,* 2005) and was chosen as a good single measure of relative temperature differences among sites to relate to single measures of drift and diet.

Substrate size, channel dimensions, and channel slope were measured in a 100-m stream reach within 1 km upstream of the drift net sampling location during the summer of 2003. Cross-channel transects were placed every 5 m. For each transect, crews measured wetted channel width (m), mean wetted depth (cm; Overton *et al.,* 1997), and dominant substrate size characteristics within a 10-cm-diameter circle at 7 points evenly spaced across the wetted width. Substrate categories were defined using an Udden-Wentworth grain-size scale following Buffington & Montgomery (1999a): 1 = silt <1/16 mm, 2 = sand 1/16–2 mm, 3 = gravel 2–64 mm, 4 = cobble 64–256 mm, 5 = boulder >256 mm or bedrock. Channel slope was measured with a hand level and stadia rod.

From these data, we calculated reach-averaged indices of substrate diversity and substrate mobility. Relative substrate diversity (evenness) was calculated from the normalized Shannon-Wiener index (Zar, 1999), while substrate mobility was determined from the Shields (1936) stress. Shields stress (τ^*) is a dimensionless mobility index defined as the ratio of applied shear stress (tractive force per unit bed area) to that resisting substrate motion (submerged particle weight per unit bed area)

$$\tau^* = \tau_0 / [(\rho_s - \rho) g D_i] \quad (1)$$

where τ_0 is the reach-average shear stress determined as a depth-slope product (ρghS, where ρ is fluid density (1000 kg/m^3), g is gravitational acceleration, h is reach-average flow depth, and S is reach-average channel slope), ρ_s is sediment density (2650 kg/m^3), and D_i is the midpoint of the substrate size class observed at a given transect point within a study reach. The reach-average shear stress is further corrected for substrate roughness (Wiberg & Smith, 1991; Buffington & Montgomery, 1999b) due to large particle sizes relative to flow depths at the study sites. Mobility is expressed here as the proportion of the bed surface having Shields stresses greater than the critical value for substrate motion (0.03; Buffington & Montgomery, 1997). In other words, it is the proportion of the bed that is mobile. Flow measurements and mobility calculations were conducted during summer months after spring runoff diminished. Consequently, mobility values represent substrate mobility under moderate to low flow conditions.

Data Analysis

All streams were fish-bearing, and measured fish densities varied among sites (A. Rosenberger & J. Dunham, unpubl. data). Because fish density in the study sites did not relate consistently with disturbance history or correlate with aquatic macroinvertebrate drift density (A. Rosenberger & J. Dunham, unpubl. data), it was considered a source of random variation in this field experiment. In addition, because our sample sizes were small ($n = 3$ per disturbance type), the statistical power of comparisons was limited; however, means for each disturbance category with standard errors are reported to give a general idea of differences among and within categories. We used Pearson correlations to examine relationships between drift and diet characteristics and habitat features. Analyses were performed using SAS (SAS® Version 8.02, Cary, NC).

Results

Drift

For summer samples of all streams, particularly burned and reorganized streams, the families Simuliidae and Chironomidae (both of the Order Diptera) were the most frequently observed aquatic macroinvertebrate taxa in the drift (Table 3.2.II 2). For unburned streams, members of the genus *Optioservus* (Family Elmidae, Order Coleoptera) and *Baetis tricaudatus* (Family Baetidae, Order Ephemeroptera) were also common. In burned streams, we found that *B. tricaudatus* were most abundant in the drift, followed by members of the genera *Optioservus* and *Lepidostoma* (Family Lepidostomatidae, Order Trichoptera). Dipterans were most common in the drift in burned and reorganized streams. In addition to chironomids and simuliids, *Brachycentrus americanus* (Family Brachycentridae, Order Trichoptera) and members of the genus *Optioservus* also were frequently observed in these stream types. In the autumn samples, *B. tricaudatus* and chironomids were frequently observed in all stream types. Simuliids were more common in the burned and reorganized streams in the fall than the other two disturbance types (Table 3.2.II 2).

Characteristics of aquatic macroinvertebrate drift, including summer biomass density, were highly variable among streams, and showed greater variability within than among disturbance types (Figure 3.2.II 2). Contrary to expectations, burned streams, which are intermediate in canopy cover between the other two disturbance types (Table 3.2.II 3), did not have the highest biomass densities (Figure

3.2.II 2). The highest drift biomass density was observed in Trail Creek, an unburned stream with canopy openness comparable to that of the burned streams (Table 3.2.II 3). For all disturbance types combined, we observed a general decrease in drift biomass density in the autumn months (Figure 3.2.II 2).

Although there were no clear effects of disturbance type on drift biomass, more subtle differences in aquatic macroinvertebrate drift characteristics were observed among disturbance types, which could be related to differences in habitat characteristics among sites. Average individual body size of aquatic macroinvertebrate drift and standardized measures of taxonomic richness during the summer overlapped among unburned and burned streams, but were lowest in burned and reorganized streams (Table 3.2.II 4). These patterns may be temperature-related. Maximum summer temperatures overlapped among sites in unburned and burned streams; however, burned and disturbed sites had the warmest temperatures (Table 3.2.II 3). Maximum summer temperatures in the sites were negatively correlated with summer measures of average individual body size (Pearson $r = -0.77$, $P = 0.02$) and rarefied taxonomic richness (Pearson $r = -0.76$, $P = 0.02$) of drifting aquatic macroinvertebrates (Figure 3.2.II 3). For the fall samples, differences between disturbance types in individual body size of aquatic macroinvertebrates were minimal; however, the summer pattern of lowest taxonomic richness in burned and reorganized sites continued into the autumn months (Table 3.2.II 4). Although there was little variability among sites or disturbance types in substrate diversity, burned and reorganized streams had generally less mobile beds than the other two disturbance types (Table 3.2.II 2). However, substrate evenness and mobility did not correlate with rarefied summer taxonomic richness (Pearson $r = -0.53$, $P = 0.85$ and $r = 0.46$; $P = 1.0$, respectively).

Diet

Overall, simuliids were most common in the diets of rainbow trout in all streams for the summer sample (Table 3.2.II 3). Also common in all streams were small mayflies, *B. tricaudatus*, ants (Family Formicidae, Order Hymenoptera), and chironomids. For unburned streams only, parasitoid wasps (Order Hymenoptera) were frequently observed in rainbow trout diets.

During autumn, chironomids were most common in rainbow trout diets in unburned streams, followed by *Apatania* (Family Apataniinae, Order Trichoptera) and aphids (Family Aphidae, Order Homoptera). In burned streams, chironomids were frequently observed in trout diets, followed by *Heterlimnius* (Family Elmidae, Order Coleoptera). In burned and reorganized streams, *Lepidostoma* were most common in the diets, followed by chironomids (Table 3.2.II 3).

Characteristics of trout stomach contents varied among streams (Table 3.2.II 5). Contrary to expectations, for the summer months, there was more variability within disturbances categories than among them in terms of the proportion of terrestrial insects in trout diets (Table 3.2.II 5). However, for the fall sample, terrestrial insects were proportionally more dominant in the stomach contents than aquatic insects for unburned streams only; in burned streams and burned and reorganized streams, terrestrials were less dominant than aquatic insects. This may be related to differences in canopy cover among disturbance types. There was a significant relationship between canopy cover and the proportion of terrestrial insects in rainbow trout diets in the fall (Pearson $r = 0.72$, $P = 0.03$); however, this relationship was driven by the dominance of terrestrial insects in the diets of rainbow trout in unburned streams compared to the other two disturbance types (Figure 3.2.II 4). There was a general decrease in body size and taxonomic richness of summer aquatic macroinvertebrates in trout stomach contents in burned and reorganized streams compared to the other channel types (Table 3.2.II 5), similar to the pattern observed in the drift. However, unlike the drift sample, the body size of summer aquatic macroinvertebrates in trout stomach contents did not significantly correlate with maximum

summer temperature (Pearson $r = -0.47$, $P = 0.21$). We did observe, however, a negative correlation between aquatic taxonomic richness in trout stomach contents and maximum summer temperature (Pearson $r = -0.73$, $P = 0.03$), just as we had in the drift. As with aquatic macroinvertebrate drift, reach-average measures of substrate evenness and mobility were not associated with summer aquatic taxonomic richness in rainbow trout stomach contents (Pearson $r = -0.73$, $P = 0.14$ and Pearson $r = 0.40$, $P = 1.0$, respectively).

Discussion

Previous studies indicate that macroinvertebrate communities in streams influenced by severe wildfire can return to pre-impact conditions within a decade (Minshall, 2003). This recovery could support associated recovery of aquatic predators, such as trout. At intermediate time scales (10-100 years), effects of wildfire on macroinvertebrates and predator-prey dynamics are likely to be subtle and indirect (Minshall, 2003). This was the case in our study. We found that biomass density of aquatic macroinvertebrate drift was unrelated to channel disturbance history or associated habitat features. Instead, aquatic macroinvertebrates in the drift were generally smaller and less rich taxonomically in warmer streams. Taxonomic richness was also lower in the diets of rainbow trout in warmer streams. Sites with a history of both fire and channel reorganization were warmer than sites in burned or unburned streams, and therefore exhibited the strongest biological response. These results indicate that stream temperature was a primary factor influencing macroinvertebrate drift characteristics, while disturbance history was secondary. Stronger effects of disturbance history on stream temperature are more apparent in landscape-scale studies with larger sample sizes that can better account for confounding factors, such as elevation and drainage area (Dunham *et al., in press*); these effects may be masked in smaller, localized, samples, such as those used in the current study, which show overlap in maximum temperatures between unburned and burned sites. This underscores the importance of relating underlying physical conditions rather than broad treatment classifications (e.g., unburned, burned, and burned and reorganized streams) to observed biotic patterns for understanding ecosystem response. In contrast, characteristics of fish diets in the autumn did show an association with channel disturbance category. The significant positive correlation between the proportions of terrestrial insects in rainbow trout diets with measures of overhead canopy in autumn months was driven by the dominance of terrestrial insects in rainbow trout diets in unburned streams.

Although substrate features are important determinants of aquatic macroinvertebrate taxon diversity (Reice, Wissmar, & Naiman, 1990; Matthaei, Uehlinger, & Frutiger, 1997; McCabe & Gotelli, 2000), no relationship was observed in our study. This may be due to coarse classification of the range of grain sizes present; potentially important differences in the abundance of gravel sizes (2-64 mm, those most relevant for macroinvertebrates; Cummins & Lauf, 1969) were not discriminated.

We originally hypothesized that burned streams with intermediate canopy cover would have the highest aquatic macroinvertebrate drift densities, presumably due to increased autochthonous input from greater solar radiation due to the loss of forest trees together with allochthonous input from intact deciduous streamside vegetation. The lack of support for this hypothesis in our study differs from other studies where loss of riparian forest resulted in increased stream primary productivity, fueling macroinvertebrate productivity (Fuller, Roelofs, & Fry, 1986; Hill, Ryon, & Schilling, 1995). Drift can be highly variable, and our methods may have been inadequate for measuring differences among stream disturbance categories.

However, several plausible mechanisms could also account for the lack of a strong effect of channel disturbance history on drift biomass density. Increased algal productivity resulting from increased sunlight may have been consumed by juvenile tailed frogs (*Ascaphus montanus*), which are abundant

in these streams (Dunham *et al., in press*), before entering the macroinvertebrate food web (Kiffney & Richardson, 2001). Alternately, differences in canopy openness between unburned and disturbed streams may not have been enough to elicit a significant response in primary productivity. Nutrient input rather than solar radiation may be limiting primary productivity (Brown, Gahler, & Marston, 1973; Fuller, Kennedy, & Nielsen, 2004), particularly in streams with severely burned catchments. The increase in nutrients that has been observed in streams immediately after wildfire (Spencer, Gabel, & Hauer, 2003) may be followed by a long-term decrease if nutrients in the watershed are sequestered by recovering upland vegetation before reaching the stream channel (Bormann & Likens, 1994; Minshall, Brock, & Varley, 1989). Finally, increased temperatures associated with loss of riparian vegetation could offset the benefits of increased primary production. Earlier emergence in warmer systems could result in loss of aquatic macroinvertebrates that would otherwise occur in the drift during the summer months (Vannote & Sweeney, 1980; Hogg & Williams, 1996).

Despite lack of differences between disturbance types in drift biomass density, more subtle patterns of macroinvertebrate drift and trout diet suggest that warmer streams with a history of wildfire and channel reorganization may present greater costs for trout in terms of food quality, reliability, and terrestrial input. The smaller prey observed in burned and reorganized streams may be more difficult for fish to capture due to shorter reaction distances or increased handling time (Ware, 1972), potentially increasing time spent foraging to meet the higher metabolic demands from warmer temperatures (Linton *et al.,* 1998; Railsback *et al.,* 2005). Increased activity to avoid starving may render trout more vulnerable to predators (Lima, 1998, Hoejesjoe, Johnsson, & Axelsson, 1999) or disease from stress (Bly, Quiniou, & Clem, 1997; Suomalainen, Tiirola, & Valtonen, 2005). Further, fish in warmer streams may face greater temporal variability in food availability if taxonomic richness is related to stability in the food resource (e.g., Brown, 2003), and it is in warmer streams that fish most require an abundant, consistent food supply (Grove, Loizides, & Nott, 1978). Finally, rainbow trout in burned streams with and without channel reorganization had fewer terrestrial macroinvertebrates in their diet than in unburned streams during autumn. It is during this time, when aquatic macroinvertebrate drift is reduced and trout are storing fat for winter, that terrestrial input to fish diets is most important (Wipfli, 1997; Nakano & Murakami, 2001; but see Romero, 2004).

Although responses of terrestrial macroinvertebrates to fire have been found to vary with forest composition, fire severity, and species (McCullough, Werner, & Neumann, 1998), there is, to our knowledge, no information on the effects of postfire forest recovery on seasonal abundance and diversity of terrestrial insects entering stream drift. A future avenue for investigation would be to examine if the presence of mature, streamside, coniferous forest, which is lacking in both burned and burned and reorganized streams, is particularly important for supplying terrestrial macroinvertebrates (e.g., aphids) to drift during autumn months when deciduous riparian vegetation is losing foliage. A study of how disturbance affects seasonal input of terrestrial macroinvertebrates into stream drift and how it affects trout should also account for flexible feeding behaviors of salmonids that may compensate for this loss. Trout in streams facing less drift availability during the cooler autumn months when metabolic demands are less could switch behaviors to nighttime feeding (Railsback *et al.,* 2005) or benthic foraging to compensate (Baxter *et al.,* 2004).

Results of our study reveal the potential for wildfire to indirectly influence prey taxonomic composition, predator-prey interactions, and perhaps other associated ecosystem processes (e.g., Wootton, Parker, & Power, 1996; Baxter, Fausch, & Saunders, 2005) a decade after disturbance. However, it appears that species distributions (Dunham *et al., in press*) and drift biomass have recovered over shorter time scales. We have limited understanding of the effects of wildfire and channel reorganization on stream ecosystem processes because few studies have examined how

wildfire influences energy input, energy flow, species interactions, or food webs in streams, particularly at intermediate time scales (Mihuc & Minshall, 1995; Minshall, 2003). Yet we know these processes drive aggregate responses such as species occurrence, abundance, and population productivity (Evans, Warren, & Gaston, 2005). Our study suggests that broader characteristics of stream ecosystems recover more quickly than the underlying processes from which they are derived. A lack of unified response of stream biota to wildfire and channel reorganization in wholesale features such as distribution and abundance (Minshall, 2003; Dunham *et al.,* 2003), together with evidence for more subtle impacts of wildfire disturbance on riparian vegetation and temperature, highlight the complexity of interactions among physical and biological processes and how they contribute to variable ecosystem responses to wildfire.

Acknowledgements

Funding for this work was provided by the National Fire Plan and the U.S. Forest Service Rocky Mountain Research Station, in cooperation with the Boise National Forest, upon which this work was conducted. We thank Michael Kellett, Dona Horan, Joseph Benjamin, Brooke Nelson, Dan Bolin, Ciara Cusack, Tobias Jongeward, Tim Arrington, Kristin Bott, Aaron Golart, Kristen Bednarczyk, Mary Beatty, and Garet Tessmer for assistance in the field. We also thank Robert Wisseman for his extraordinary efforts in carefully processing drift and diet samples and David Nagel for offering his GIS expertise to provide canopy cover data for analysis. Special thanks to Barbara Gutierrez and Bruce Rieman for expert technical advice and comments on this study throughout its progress. We also thank Dave Turner for advice on data analysis and interpretation. We thank Loretta Orgill, Wayne Minshall, Karl Polivka, and two anonymous reviewers for helpful advice on earlier versions of this manuscript.

References (3.2.II)

Baxter C.V., Fausch K.D., Murakami M., & Chapman P.L. (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, **85,** 2656-2663.

Baxter C.V., Fausch K.D., & Saunders W.C. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, **50**, 201-220.

Benda L., Miller D., Bigelow P., & Andras K. (2003) Effects of post-wildfire erosion on channel environments, Boise River, Idaho. *Forest Ecology and Management*, **178,** 105-149.

Benda L., Miller D., Dunne T., Agee J., & Reeves G. (1998) Dynamic landscape systems. In: *River ecology and management: lessons from the Pacific Coastal Ecoregion.* (Eds R. Naiman & R. Bilby), pp. 261-288. Springer, New York, New York.

Beschta R.L., Bilby R.E., Brown G.W., Holtby L.B., & Hofstra T.D. (1987) Stream temperature and aquatic habitat: fisheries and forestry interactions. In: *Streamside Management: Forestry and Fishery Interactions* (Eds E.O. Salo & T.W. Cundy), pp. 191-232. Contribution No. 57, Institute of Forest Resources, University of Washington, Seattle, Washington.

Bisson P.A., Rieman B.E., Luce C., Hessburg P.F., Lee D.C., Kershner J.L., Reeves G.H., & Gresswell R.E. (2003) Fire and aquatic ecosystems of the western USA: current knowledge and key questions. *Forest Ecology and Management*, **178**, 213-229.

Bly J.E., Quiniou S.M., & Clem L.W. (1997) Environmental effects on fish immune mechanisms. *Development of Specifications for Biotechnology Pharmaceutical Products*, **90**, 33–43.

Bormann F.H. & Likens G.E. (1994) *Pattern and process in a forested ecosystem: disturbance, development and the steady state based on the Hubbard ecosystem study.* Springer-Verlag, New York, New York.

Brown B.L. (2003) Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters*, **6**, 316–325.

Brown G.W., Gahler A.R., & Marston R.B. (1973) Nutrient losses after clear-cut logging and slash burning in the Oregon coast range. *Water Resources Research*, **9**, 1450-1453.

Buffington J.M. & Montgomery D.R. (1997) A systematic analysis of eight decades of incipient motion studies, with special reference to gravel-bedded rivers. *Water Resources Research*, **33**, 1993–2029.

Buffington J.M. & Montgomery D.R. (1999a) A procedure for classifying textural facies in gravel-bed rivers. *Water Resources Research*, **35**, 1903–1914.

Buffington J.M. & Montgomery D.R. (1999b) Effects of sediment supply on surface textures of gravel-bed rivers. *Water Resources Research*, **35**, 3523–3530.

Bunge J. & Fitzpatrick M. (1993) Estimating the number of species; a review. *Journal of the American Statistical Association*, **88**, 364–373.

Burgherr P. & Meyer E.I. (1997) Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv fur Hydrobiologie*, **139**, 101–112.

Burton T.A. (2005) Fish and stream habitat risks from uncharacteristic wildfire: observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. *Forest Ecology and Management*, **211**, 140-149.

Camp A., Oliver C., Hessburg P., & Everett R. (1997) Predicting late-successional fire refugia predating European settlement in the Wenatchee Mountains. *Forest Ecology and Management*, **95**, 63–77.

Caton L. (1991) Improved subsampling methods for the EPA Rapid Bioassessment benthic protocols. *Bulletin of the North American Benthological Society*, **8**, 317-319.

Culp J.M., Walde S.J., & Davies R.W. (1983) Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1568–1574.

Cummins K.W. & Lauf G.H. (1969) The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia*, **34**, 145-181.

Cummins K.W., Wilzbach M.A., Gates D.M., Perry J.B., & Taliaferro W.B. (1989) Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. *BioScience*, **39**, 24–30.

Death R.G. (2003) Spatial patterns in lotic invertebrate community composition: is substrate disturbance actually important? *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 603–611.

Dunham J.B., Young M.K., Gresswell R.E., & Rieman B.E. (2003) Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. *Forest Ecology and Management*, **178**, 183-196.

Dunham J., Chandler G., Rieman B., & Martin D. (2005) Measuring stream temperature with digital data loggers: A user's guide. General Technical Report. RMRSGTR-150WWW. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Dunham J.B., Rosenberger A.E., Luce C.H., & Rieman B.E. *In press*. Long-term influences of wildfire on stream temperature: spatio-temporal patterns and the distribution of fish and amphibians. *Ecosystems*.

Dwire K.A. & Kauffman J.B. (2003) Fire and riparian ecosystems in landscapes of the western USA. *Forest Ecology and Management*, **178**, 61–74.

Evans K.L., Warren P.H., & Gaston K.J. (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1-25.

Fausch K.D., Torgersen C.E., Baxter C.V., & Li H.W. (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience*, **52**, 483-498.

Frutiger A. & Imhof A. (1997) Life cycle of *Dinocras cephalotes* and *Perla grandis* (Plecoptera: Perlidae) in different thermal regimes. In: *Ephemeroptera, Plecoptera: biology-ecology-systematics* (Eds P. Landolt & M. Sartori), pp. 34–43. MTL-Mauron and Tinguely Lachat SA, Fribourg. Switzerland.

Fuller R.L., Kennedy B.P., & Nielsen C. (2004) Macroinvertebrate responses to algal and bacterial manipulations in streams. *Hydrobiologia*, **523**, 113-126.

Fuller R.L., Roelofs J.L., & Fry T.F. (1986) The importance of algae to stream invertebrates. *Journal of the North American Benthological Society*, **5**, 290–296.

Gotelli N.J. & Colwell R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Gresswell R.E. (1999) Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society*, **128**, 193-221.

Grove D.J., Loizides L.G., & Nott J. (1978) Satiation amount, frequency of feeding and gastric emptying rate in *Salmo gairdneri*. *Journal of Fish Biology*, **12**, 507-516.

Hill W.R., Ryon M.G., & Schilling E.M. (1995) Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology*, **76**, 1297–1309.

Hoejesjoe J., Johnsson J.I., & Axelsson M. (1999) Behavioural and heart rate responses to food limitation and predation risk: an experimental study on rainbow trout. *Journal of Fish Biology*, **55**, 1009-1019.

Hogg I.D. & Williams, D.D. (1996) Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology*, **77**, 395–407.

Kawaguchi Y. & Nakano S. (2001) Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology*, **43**, 303–316.

Kawaguchi Y., Yoshinori T., & Nakano S. (2003) Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology*, **84**, 701–708.

Kiffney P.M. & Richardson J.S. (2001) Interactions among nutrients, periphyton, and invertebrate and vertebrate (*Ascaphus truei*) grazers in experimental channels. *Copeia*, **2001**, 422-429.

Li H.W., Lamberti G.A., Pearsons T.N., Tait C.K., Li J.L., & Buckhouse J.C. (1994) Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. *Transactions of the American Fisheries Society*, **123**, 627-640.

Lima S.L. (1998) Stress and decision-making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215–290.

Linton T.K., Morgan I.J., Walsh P.J., & Wood C.M. (1998) Chronic exposure of rainbow trout (*Oncorhynchus mykiss*) to simulated climate warming and sublethal ammonia: a year-long study of their appetite, growth, and metabolism. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 576-586.

Lytle D.A. & Poff N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, **19**, 94-100.

Matthaei C.D., Uehlinger U., & Frutiger A. (1997) Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, **35**, 233-248.

McCabe D.J. & Gotelli N.J. (2000) Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia*, **124**, 270–279.

McCullough D.G., Werner R.A., & Neumann D. (1998) Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology*, **43**, 107-127.

Meyer G.A., Wells S.G., & Jull A.J.T. (1995) Fire and alluvial chronology in Yellowstone National Park: Climate and intrinsic controls on Holocene geomorphic processes. *Geological Society of America Bulletin*, **107**, 1211-1230.

Mihuc T.B. & Minshall G.W. (1995) Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. *Ecology*, **76,** 2361-12372.

Minshall G.W., Brock J.T., & Varley J.D. (1989) Wildfires and Yellowstone's stream ecosystems: a temporal perspective shows that aquatic recovery parallels forest succession. *BioScience*, **39**, 707–715.

Minshall G.W., Robinson C.T., Lawrence D.E., Andrews D.A., & Brock J.T. (2001) Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbance by wildfire. *International Journal of Wildland Fire*, **10**, 201–213.

Minshall G.W., Royer T.V., & Robinson C.T. (2001) Response of the Cache Creek macroinvertebrates during the first 10 years following disturbance by the 1988 Yellowstone wildfires. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1077–1088.

Minshall G.W. (2003) Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management*, **178**, 155-162.

Montgomery D.R. (1999) Process domains and the river continuum. *Journal of the American Water Resource Association*, **35**, 397-410.

Nakano S. & Murakami M. (2001) Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 166–170.

Overton K.C., Wolrab S.P., Roberts B.C., & Radko M.A. (1997) R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory procedures handbook. General Technical Report INT-GTR-346, USDA Forest Service, Ogden, Utah.

Perry R.W., Bradford M.J., & Grout J.A. (2003) Effects of disturbance on contribution of energy sources to growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) in boreal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 390-400.

Pierce J.L., Meyer G.A., & Jull A.J.T. (2004) Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. *Nature*, **432**, 87-90.

Pilliod D.S., Bury R.B., Hyde E.J., Pearl C.A., & Corn P.S. (2003) Fire and amphibians in North America. *Forest Ecology and Management*, **178**, 163-182.

Reeves G.H., Benda L.E., Burnett K.M., Bisson P.A., & Sedell J.R. (1995) A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadramous salmonids in the Pacific Northwest. In: *Proceedings of the American Fisheries Society Symposium on Evolution and the Aquatic Ecosystem* (Ed. J. Nielsen J.), pp. 334-349. Vol. 17. Bethesda, Maryland.

Reice S.R., Wissmar R.C., & Naiman R.J. (1990) Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management*, **14**, 647–659.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B., & Wissmar R.C. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433-455.

Railsback S.F., Harvey B.C., Hayse J.W., & LaGory K.E. (2005) Tests of theory for diel variation in salmonid feeding activity and habitat use. *Ecology*, **86**, 947-959.

Rogers L.E., Buschbom R.L., & Watson C.R. (1977) Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America*, **70**, 51–53.

Romero N. (2004) Seasonal influences on food availability and diet of coastal cutthroat trout in relation to riparian vegetation. MS Thesis, Oregon State University, Oregon.

Sample B.E., Cooper R.J., Greer R.D., & Whitmore R.C. (1993) Estimation of insect biomass by length and width. *American Midland Naturalist*, **129**, 234–240.

Shields A. (1936) Application of similarity principles and turbulence research to bed-load movement (original in German). In: Hydrodynamics Laboratory Report 167, (Trans. Ott W.P. & Van Uchelen J.C.), U.S. Department of Agriculture, Soil Conservation Service Cooperative Laboratory, California Institute of Technology, Pasedena, California.

Smock L.A. (1980) Relationships between body size and biomass of aquatic insects. *Freshwater Biology*, **10**, 375–383.

Spencer C.N., Gabel K.O., & Hauer F.R. (2003) Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management*, **178**, 141-154.

Suomalainen L.R., Tiirola M.A., & Valtonen E.T. (2005) Influence of rearing conditions on Flavobacterium columnare infection of rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Diseases*, **28**, 271-277.

Taylor A.H. & Skinner C.N. (1998) Fire regimes and landscape dynamics in a late-successional reserve in the Klamath Mountains, California, USA. *Forest Ecology and Management*, **11**, 285–301.

Vannote R.L. & Sweeney B.W. (1980) Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, **115**, 667–695.

Ware D.M. (1972) Predation by rainbow trout (*Salmo gairdneri*): The influence of hunger, prey density, and prey size. *Journal of the Fisheries Research Board of Canada*, **30**, 787-797.

Westerling A.L., Hidalgo H.G., Cayan D.R., & Swetnam T.W. (2006) Warming and earlier spring increases western U.S. forest wildfire activity. *Science*, **313**, 940-943 .

Wiberg P.L. & Smith J.D. (1991) Velocity distribution and bed roughness in high-gradient streams. *Water Resources Research*, **27**, 825–838.

Wipfli M.S. (1997) Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1259–1269.

Wipfli M.S. & Gregovich D.P. (2002) Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. *Freshwater Biology*, **47**, 957-969.

Wondzell S.M. & King J.G. (2003) Postfire erosional processes in the Pacific Northwest and Rocky Mountain regions. *Forest Ecology and Management* **178**, 75-88.

Wootton J.T., Parker M.S., & Power M.E. (1996) Effects of disturbance on river food webs. *Science*, **273**, 1558–1561.

Zar J.H. (1999) *Biostatistical Analysis*. Prentice Hall, New Jersey.

Table 3.2.II 1 Characteristics of sampling locations[1] for macroinvertebrate drift and trout diet and characteristics of trout sampled for stomach contents.

	Unburned			Burned			Burned and reorganized		
Site Features	BV	LM	TL	CW	HU	LO	SFS	TR	WR
Contributing area (ha)	1451	4550	1954	3872	1142	1544	3178	1000	1022
Elevation at sampling location (m)	1341	1398	1488	1139	1357	1415	1695	1450	1489
Proportion of channel moderately to severely burned	0	0	0	1.00	0.87	0.78	0.62	0.97	1.00
Rainbow trout sampled for stomach contents									
Summer *n*	9	10	11	9	9	6	11	10	10
Size range (mm)	72–118	77–144	72–157	138–175	62–146	128–165	60–154	69–154	102–153
Autumn *n*	8	10	10	12	8	11	8	10	10
Size range (mm)	76–143	88–142	82–144	90–163	89–119	82–149	76–130	82–144	69–154

[1] *Undisturbed streams: Beaver (BV), Lost Man (LM), and Trail (TL) creeks; burned streams: Cottonwood (CW), Hungarian (HU), and Lost (LO) creeks (all burned by the Rabbit Creek Fire, 1994); burned and disturbed streams: South Fork Sheep Creek (SFS; Foothills Fire, 1992) and Trapper (TR), and Wren (WR) creeks (Rabbit Creek Fire, 1994).*

Table 3.2.II 2 Common taxa in aquatic macroinvertebrate drift and rainbow trout diet, presented as the proportion of the total abundance of individuals enumerated in drift and in trout stomach contents. Data from streams with similar wildfire histories (undisturbed, burned, and burned and reorganized) are lumped.

Aquatic macroinvertebrate drift

	Summer			Autumn		
Taxa	Unburned	Burned	Burned and reorganized	Unburned	Burned	Burned and reorganized
Chironomidae	0.12	0.19	0.37	0.21	0.27	0.11
Baetis tricaudatus, Dodds	0.24	0.18	0.03	0.27	0.14	0.38
Simuliidae	0.11	0.09	0.17	0.04	0.08	0.19
Optioservus	0.08	0.10	0.09	0.04	0.03	0.06
Brachycentrus americanus, Banks	0.01	0	0.17	0.01	0.01	0.07
Lepidostoma	0.01	0.09	0.05	<0.01	0	0.05
Heterlimnius	0.04	0.04	0	0.04	0.08	0
Ephemerella inermis, Eaton	0	0	0	0.03	0.10	0.02
Serratella tibialis, McDunnough	0.11	0	0	0	0	0
Capniidae	0	0	0	0.07	0.02	0.01
Pericoma	0	0	0	0.08	0.01	<0.01
Other	0.12	0.19	0.37	0.21	0.25	0.11

Rainbow trout diet

	Summer			Autumn		
Taxa	Unburned	Burned	Burned and reorganized	Unburned	Burned	Burned and reorganized
Simuliidae	0.54	0.33	0.75	0.04	0.02	0.05
Baetis tricaudatus	0.10	0.16	0.04	0.03	0.04	0.02
Formicidae	0.07	0.11	0.04	0.03	0.04	0.02
Chironomidae (aquatic)	0.05	0.02	0.02	0.31	0.28	0.21
Hymenoptera	0.04	0.02	0.01	0.01	<0.01	0.00
Apatania	<0.01	0.00	<0.01	0.11	0.04	0.04
Aphiidae	<0.01	0.002	<0.01	0.11	0.01	0.01
Heterlimnius	0.02	0.01	<0.01	0.02	0.13	0.00
Lepidostoma	0.00	0.00	<0.01	<0.01	0.00	0.34
Other	0.17	0.35	0.14	0.34	0.44	0.31

Table 3.2.II 3 Habitat characteristics of sampling locations from which macroinvertebrate drift and rainbow trout diet data were collected. For all habitat variables, data describe conditions at or upstream of the drift-net sampling location. Average characteristics for each disturbance category are reported below stream values followed by the standard error in parentheses.

	Unburned			Burned			Burned and Reorganized		
Habitat Features	BV	LM	TL	CW	HU	LO	SFS	TR	WR
Proportion of stream length with open canopy (1 km)	0.15	0.1	0.5	0.53	0.67	0.67	0.82	0.91	0.87
		0.25 (0.13)			0.62 (0.05)			0.87 (0.03)	
Maximum summer temperature (°C)	14.4	18.7	20.3	22.6	16.4	19.9	23.8	26.3	24.4
		17.8 (1.8)			19.6 (1.8)			24.8 (0.8)	
Substrate-size evenness (normalized S-W index)	0.70	0.72	0.83	0.80	0.72	0.78	0.80	0.80	0.71
		0.75 (0.04)			0.77 (0.02)			0.77 (0.03)	
Substrate mobility (proportion of bed with Shields stress above critical value)	0.73	0.38	0.42	0.50	0.92	0.63	0.41	0.52	0.21
		0.51 (0.11)			0.68 (0.12)			0.38 (0.09)	

Table 3.2.II 4 Characteristics of aquatic macroinvertebrate drift in Idaho streams with different burn histories for summer and fall samples. For comparative purposes, taxon-richness measures were standardized for number of individuals processed using rarefaction. Average characteristics for each disturbance category are reported below stream values followed by the standard error in parentheses.

Aquatic Macroinvertebrate Drift Characteristics		Unburned			Burned			Burned and Reorganized		
		BV	LM	TL	CW	HU	LO	SFS	TR	WR
Average body size (mg)	Summer	1.86	1.22	1.01	1.56	2.01	1.33	0.74	1.05	0.51
			1.36 (0.26)			1.63 (0.20)			0.77 (0.16)	
	Autumn	0.37	0.57	0.62	0.51	1.08	0.52	0.99	0.18	0.4
			0.52 (0.08)			0.7 (0.19)			0.52 (0.24)	
Standardized taxonomic richness	Summer	29	22	15	17	19	28	11	12	16
			22 (4)			21 (3)			13 (2)	
	Autumn	25	25	17	24	25	25	17	16	13
			22 (3)			25 (0)			15 (1)	

Table 3.2.II 5 Characteristics of rainbow trout diet in Idaho streams with different burn histories for summer and fall samples. For comparative purposes, taxon-richness measures were standardized for number of individuals processed using rarefaction. Average characteristics for each disturbance category are reported below stream values followed by the standard error in parentheses.

Rainbow trout diet Characteristics		Unburned			Burned			Burned and Reorganized		
		BV	LM	TL	CW	HU	LO	SFS	TR	WR
% terrestrial in origin	Summer	5	41	35	28	53	81	55	25	27
			27 (11)			54 (15)			36 (10)	
	Autumn	61	59	78	34	1	33	33	16	11
			66 (6)			23 (11)			20 (7)	
Average body size (aquatics, mg)	Summer	1.40	0.96	0.29	0.46	0.46	1.35	0.63	0.39	0.89
			0.88 (0.32)			0.76 (0.30)			0.64 (0.14)	
	Autumn	4.89	0.47	0.51	2.88	1.17	2.05	0.31	0.91	1.19
			1.96 (1.47)			2.03 (0.49)			0.8 (0.26)	
Standardized taxonomic richness (aquatic and terrestrial)	Summer	33	32	15	31	27	31	21	12	24
			27 (6)			30 (1)			19 (4)	
	Autumn	19	23	22	32	13	20	18	20	18
			21 (1)			22 (6)			19 (1)	
Standardized taxonomic richness (aquatics only)	Summer	24	16	5	11	14	19	9	5	13
			15 (6)			15 (2)			9 (2)	
	Autumn	14	8	9	13	7	10	6	8	8
			10 (2)			10 (2)			7 (1)	

Figure Legends (3.2.II)

Figure 3.2.II 1 (*omitted*; see Figure 3.2.I 1 – streams labeled with closed circles) Shaded elevation map of the upper Boise River Basin indicating stream locations and wildfire history. Streams highlighted in black and labeled by name are study streams. Red shading indicates wildfire and severity determined by the Boise National Forest (Darkest red = high severity; light pink = low severity; intermediate shade of red = moderate). Colors of the wildfire perimeters indicate the year of the event (black line = 1992; white line = 1994; green line = 2000; purple line = 2003). The spatial resolution of fire severity mapping was greater in 2000 and 2003.

Figure 3.2.II 2 Density of aquatic macroinvertebrate biomass in the drift of nine streams with different wildfire and disturbance histories for summer (July) and Fall (October) 48 hour sampling periods.

Figure 3.2.II 3 The relationship of maximum summer temperature with (A) average aquatic macroinvertebrate body size and (B) taxonomic richness in streams with different disturbance histories. For comparative purposes, taxonomic richness values were standardized for the number of individuals processed using rarefaction.

Figure 3.2.II 4 The relationship of canopy cover in autumn (proportion open canopy for 1 km upstream of drift net sampling locations) with the dominance of terrestrial macroinvertebrates in rainbow trout diets (proportion dry weight biomass of stomach contents of terrestrial origin) in streams with different wildfire and disturbance histories.

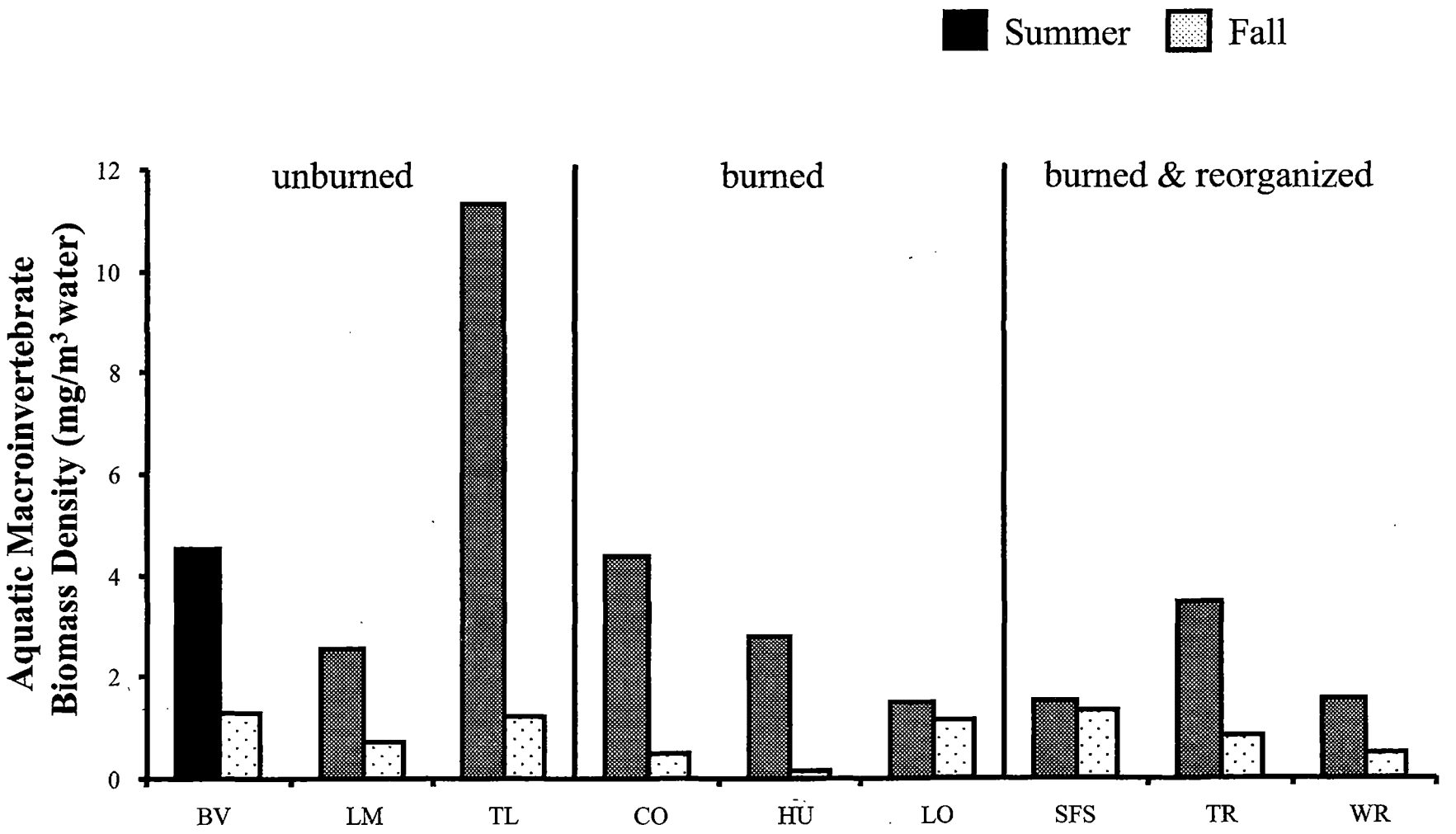


Figure 3.2.II 2

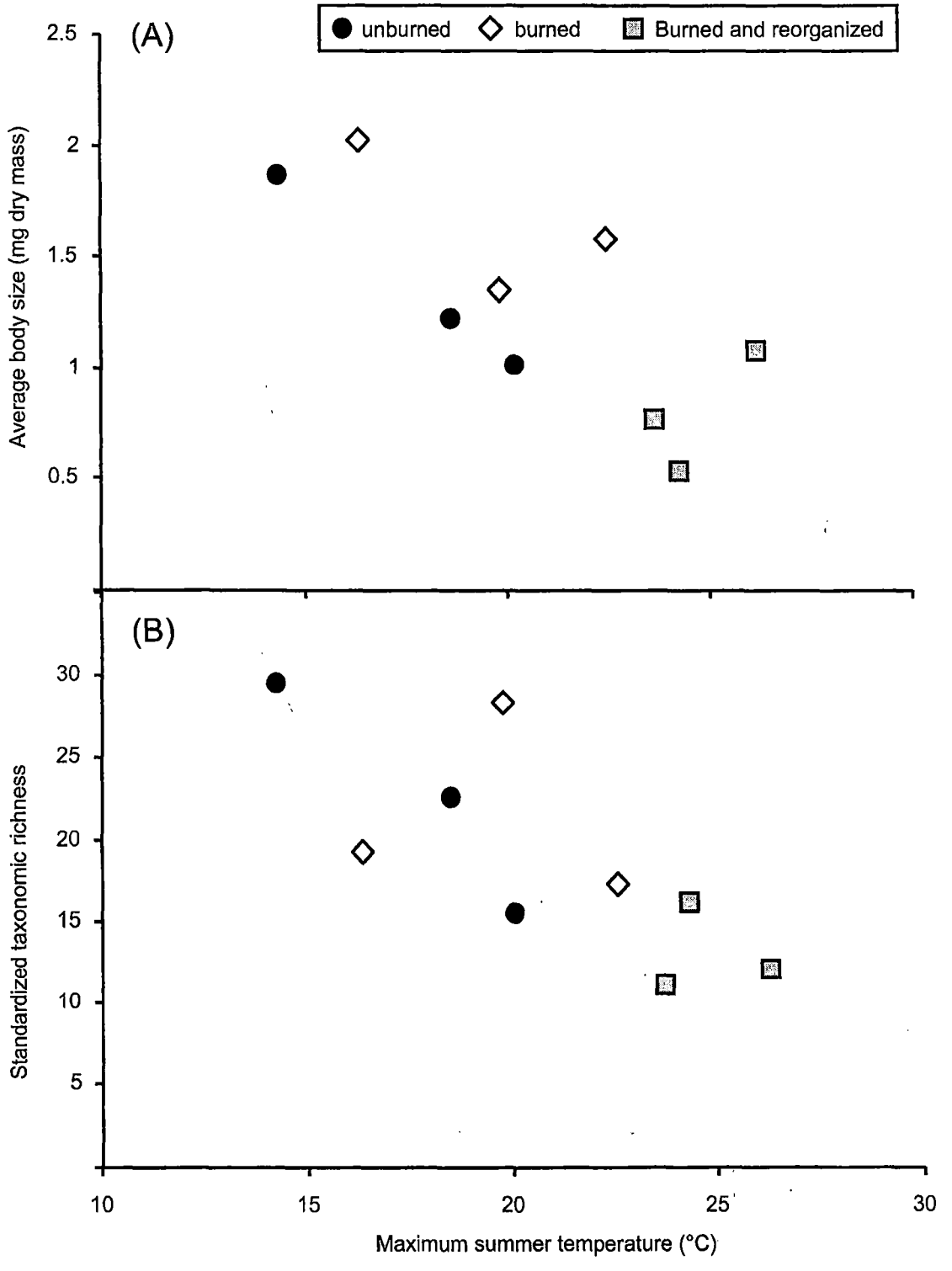


Figure 3.2.II 3

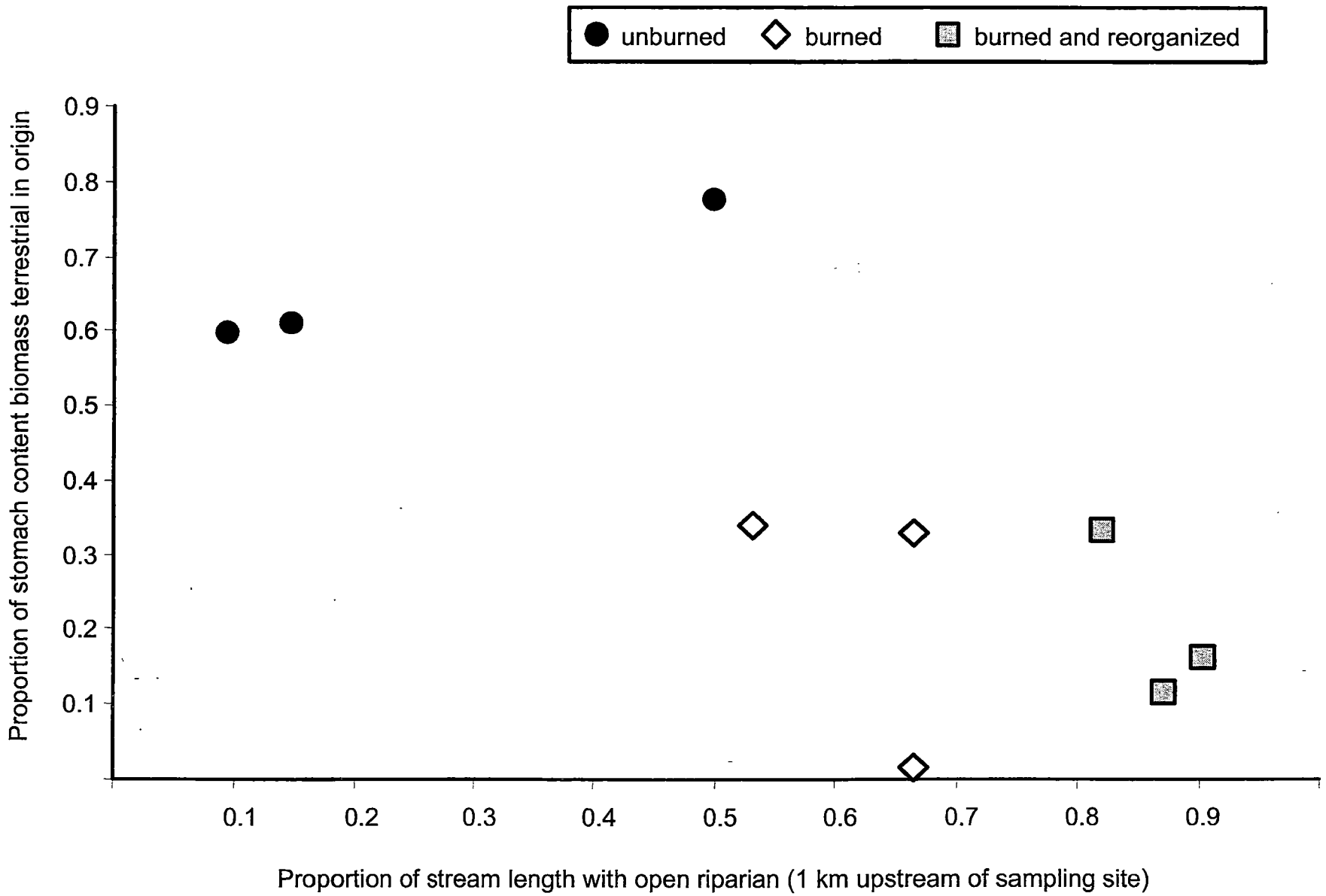


Figure 3.2.II 4

RESEARCH AREA 3 * GOAL 2 * UNPUBLISHED ANALYSIS

Effects of wildfire and channel-reorganizing events on channel morphology

Our main objectives in examining the effects of fire and post-fire disturbance on channel morphology were to: 1) compare reach-average channel morphology across the three disturbance classes in terms of standard dimensionless parameters and 2) interpret channel morphology in terms of driving fluvial processes (in this case, discharge and sediment transport) and understand the fluvial regime (physical state) associated with each disturbance class.

Although there is considerable overlap, a systematic trend of increasing slope and width-depth ratio was observed across the three disturbance classes (Figure 3.2.U. 3). The burned and disturbed channels tend to be steeper, wider and shallower, have larger substrate for a given boundary shear stress (Figure 3.2.U. 4) and, therefore, have more stable beds (Figure 3.2.U. 5).

Controls on channel morphology and interpretation of fluvial regime
A regime diagram relates channel morphology (in this case, slope and relative submergence) to driving fluvial processes (dimensionless discharge and bed load transport rate) (Figure 3.2.U. 6). The premise of the diagram is that equilibrium channel morphology is set by discharge and bed load transport rate (i.e., particular combinations of discharge and sediment transport rate yield specific values of channel morphology (contoured lines, Figure 3.2.U. 6). The regime diagram can be used to predict changes in channel morphology due to altered discharge or

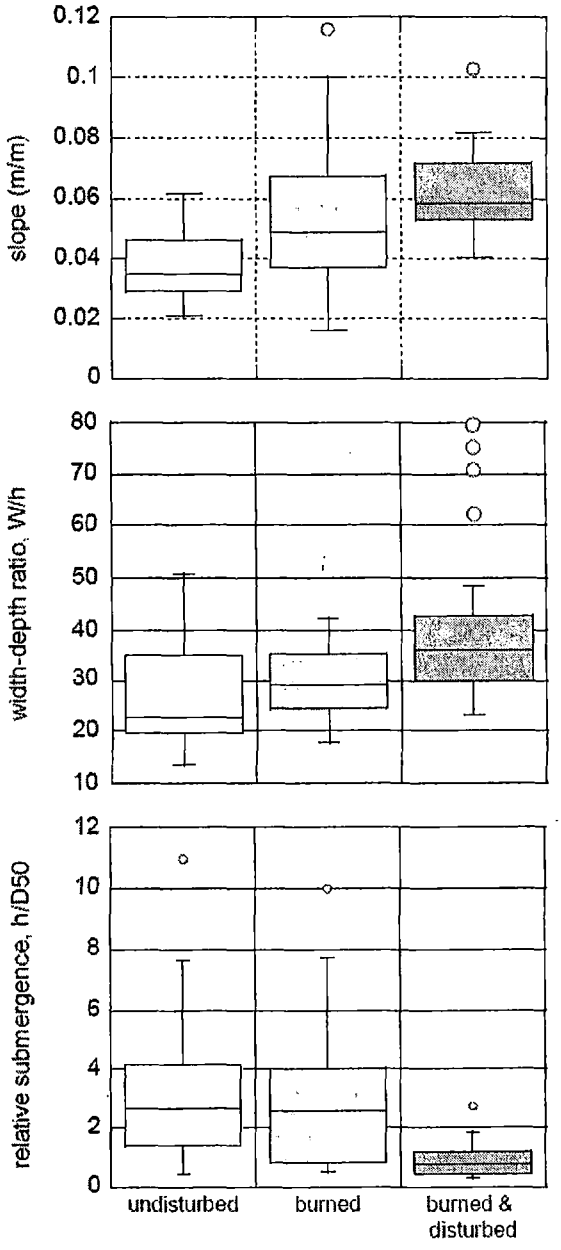


Figure 3.2.U 1 Distributions of reach-average dimensionless channel morphology a) slope, b) widthdepth ratio, and c) relative submergence (ratio of flow depth to median surface grain size).

sediment transport rate. Conversely, the diagram can also be used to assess channel regime (discharge and transport states for a given treatment).

Although there is considerable overlap, the undisturbed sites tend to have larger values of discharge and bed load transport rate than the burned and disturbed sites, with values at the burned sites roughly spanning those of the other two disturbance classes (Figure 3.2.U. 6). Lower values of discharge and bed load transport rate promote higher slopes and lower relative submergence at the burned and debris-flow sites, compared to the undisturbed sites.

Loss of vegetation and hydrophobicity from fire would be expected to cause flashier runoff and greater unit discharge (discharge per drainage area). Consequently, one might expect the disturbed sites to have higher discharges if the sites were otherwise equal in terms of basin characteristics. However, the data do not support this expectation (Figure 3.2.U. 6). Hence, the observed differences in channel morphology may result from differences in fluvial regime (inherent differences in discharge and transport rate), rather than response to fire disturbance. However, this issue deserves further investigation. In particular, drainage area should be compared, and hydraulic geometry relations should be examined across the disturbance classes to examine whether the sites are physiographically similar. Nevertheless, some of the observed differences in morphology do likely reflect response to fire disturbance, rather than inherent differences in drainage area and discharge. For example, it is possible that the larger widthdepth ratios and lower values of specific discharge observed for the burned and disturbed class are due to channel widening from debris-flow passage.

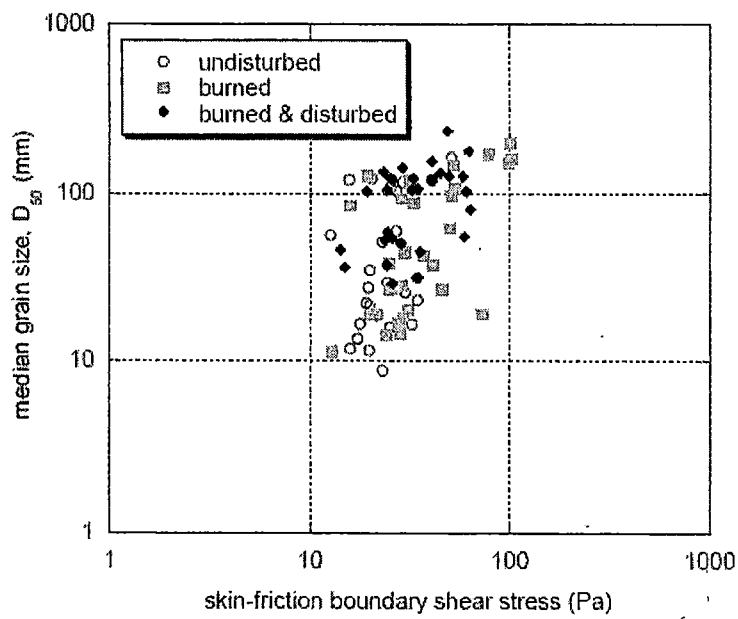


Figure 3.2.U 4. Median surface grain size relative to boundary shear stress (skin-friction component).

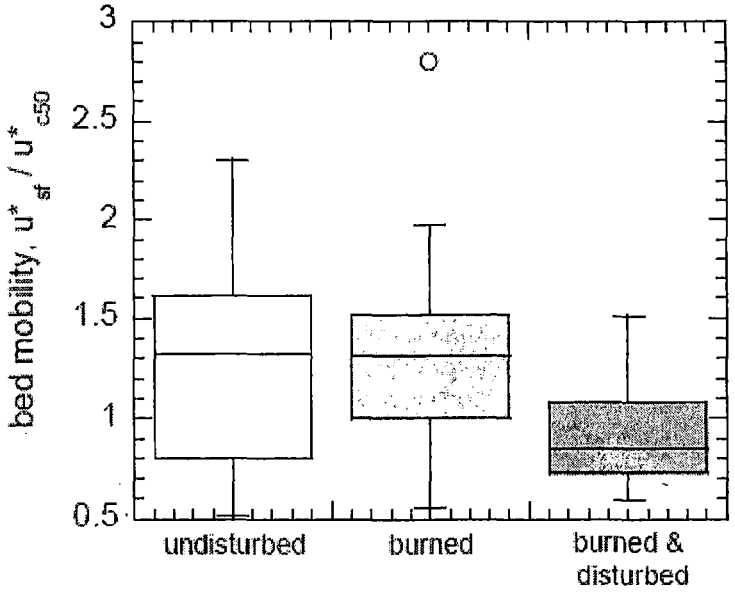


Figure 3.2.U 5. Distributions of dimensionless bed mobility (ratio of skin-friction shear velocity to critical value for motion of the median surface grain size).

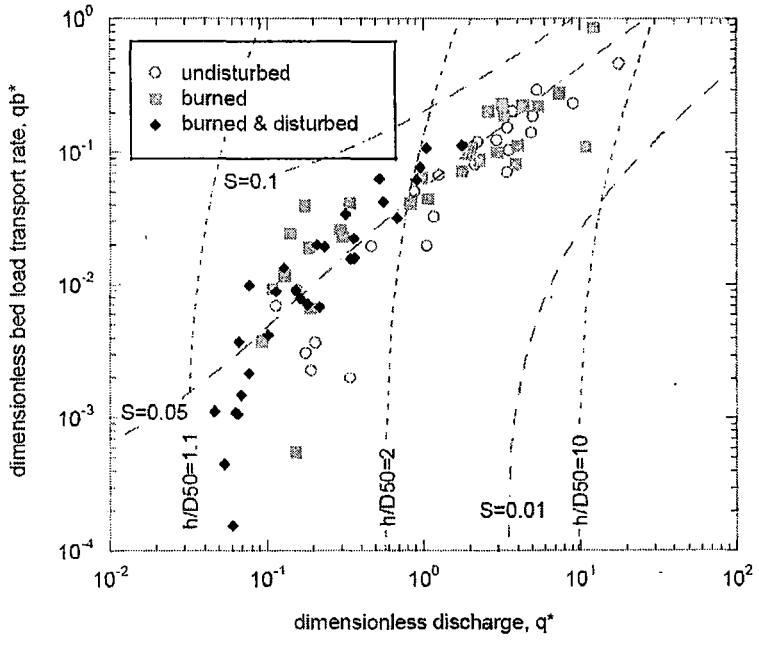


Figure 3.2.U 6. Regime diagram. Predicted contours of channel slope (S) and relative submergence (h/D_{50}, ratio of flow depth to median surface grain size) are shown.

GOAL 3: DEVELOP MODELS TO PREDICT RESPONSES OF NATIVE AND NONNATIVE AQUATIC VERTEBRATES TO FIRE AND FIRE-RELATED DISTURBANCE, AND CONSTRUCT HYPOTHESES ABOUT CAUSE-AND-EFFECT RELATIONSHIPS BETWEEN AQUATIC VERTEBRATES, FIRE, AND FIRE-RELATED DISTURBANCE.

We have completed field work, simulation work, and analyses related to this goal, and are nearing completion of the following manuscript for submission to *Ecological Applications*.

In prep. Rosenberger, A.E., J.B. Dunham, and S.F. Railsback. Population and individual responses of rainbow trout to disturbance: an integrated analysis of observation and models To be submitted to *Ecological Applications*.

The following section contains the content of the manuscript in preparation.

RESEARCH AREA 3 * GOAL 3 * PUBLICATION I (IN PREPARATION)

Population and individual responses of rainbow trout to disturbance: an integrated analysis of observation and models

Introduction

Natural disturbance is a fundamental component of functioning ecosystems, particularly flowing-water ecosystems. Aquatic organisms may show life history, behavioral, or morphological responses to disturbance that lead to resilience or even dependence on disturbance events that vary in magnitude, frequency, and intensity over time (Lytle and Poff 2003). Populations of organisms that encounter disturbance-related spatial variability in habitat conditions may demonstrate local divergence in adaptations to those conditions (Hendry 2001); however, when gene flow is high, local adaptation may be constrained (Hendry et al. 2002). Under those circumstances, a range of adaptive responses could contribute to a population-level ability to persist, or even flourish under a range of environmental conditions expected in a disturbance-prone environment (Kendall and Fox 2002). This may represent a phenotypically plastic or bet-hedging strategy adaptive for species under the long-term spatial and temporal dynamics of the aquatic ecosystem (Lytle and Poff 2003). Alternatively, long-term persistence of a metapopulation in a variable environment may be due to a diversity of inherited life history characteristics from multiple, locally-adapted populations (Hilborn et al. 2003).

To better understand mechanisms for fish population resilience to disturbance and environmental variability, researchers can investigate fish species' response through a variety of population- and individual-based measures. Population-level responses such as species distributions and abundance are typically straightforward to measure and presumably result from the cumulative impact of individual responses to environmental variability. However, relying on a limited subset of single species' response to disturbance limits our understanding of mechanisms for persistence in the face of environmental variability (Van Horne 1984; Railsback et al. 2002). Alternative, individual-based responses such as fish condition, growth, and life history characteristics such as age and size at maturity can be more illuminating; however, these data are often highly variable, intensive to collect, and also give limited information on exact linkages among environmental and biological processes (e.g., processes related to individual fitness) and resulting population-level consequences. These linkages can be complex and interactive, and multiple strategies could be adaptive in the face of disturbance or a wide range of environmental variability (McElhany et al. 2000; Mangel and Stamps 2001).

An alternative complement to field-based studies is the use of individual-based models (IBMs) to understand fish population response to simulated disturbance scenerios. IBMs can be important and useful tools for linking individual responses and behavior and their population-level consequences to environmental variability. These models allow examination of how whole-population dynamics such as population size emerge from adaptive, fitness-based behavior of individuals (Railsback 2001; Strand et al. 2002). It is

important, however, that these models are well documented, intuitive, and well rooted in reality – in essence, supported and based on actual field observations (Grimm and Railsback 2005). Ultimately, a mechanistic understanding how fish react to environmental variability as a result of disturbance requires a multi-faceted approach that integrates inferential strengths from a variety of approaches (e.g., population and individual-based field data and mechanistic modeling; Hilborn and Mangel 1997).

In this study, we examine how a decade-old history of wildfire and channel reorganization and associated alterations to their stream environment (e.g., stream temperature) affect rainbow trout *Onchorynchus mykiss* in headwater streams of the Boise National Forest, Idaho. Disturbance in the form of wildfire and channel reorganization can create lasting, landscape-scale gradients in environmental conditions, such as stream productivity (Mihuc and Minshall 1995), availability of cover in the form of wood debris (Robinson et al. 2005), and temperature regimes (Dunham et al. 2007), all of which could have individual and population-level consequences on resident biota over many generations. We expected, in a disturbance-prone environment with well-connected populations of rainbow trout, populations would exhibit both resilience to the effects of wildfire-related disturbance as well as a range of individual responses to environmental variability associated with wildfire.

For our field study, we measure population level responses of rainbow trout in headwater streams of the Boise National Forest to wildfire and channel disturbance, including distribution, abundance, and length and age distributions. We also measure individual responses in a subset of the streams, including growth, age-at-maturity, and lipid content. We then use an individual-based model to attempt to understand potential mechanisms for producing the patterns that we observed and to explore hypotheses on mechanisms behind our observations. We conducted experiments in a modeled environment developed by Railsback et al. (2001) to examine the effect of individual habitat features found to vary with fire history on specific biotic responses. The individual-based Stream Trout Research Assessment Model (inSTREAM; Railsback et al. 2001) is a simplified, controllable, and completely observable virtual environment that allows observation of population response through time. Versions of this program have been used in the past to examine the relationship between habitat and trout populations. The model has produced realistic individual- and population-level trout behavior in response to physical and ecological changes imposed on the artificial environment (Railsback et al. 2003). Because wildfire and channel reorganization affect multiple components of stream habitat (e.g., stream temperature, food availability, availability of instream shelter), it is difficult to narrow down driving factors for any observed differences in rainbow trout response. Multiple, interacting mechanisms could result in observed outcomes. The model inSTREAM was particularly suited to our questions and allowed us to narrow down potential mechanisms for observed response.

Methods

Study Area and Sampling Frame

We performed our study in headwater streams of the Middle and North forks basins of the Boise River in the summer of 2003 and fall of 2004 (Boise National Forest, central Idaho, Figure 3.3.I 1), where suitable locations are widely available in which to examine the effects of wildfire and associated channel disturbances on fish populations. Over a third of the Boise River watershed burned between 1992 and 2003, following a relatively wildfire-free period characterizing most of the 20th century. Headwater streams at mid to low evaluations for the basin were selected for study because the connectivity of headwater streams to hillslope and riparian processes make them most vulnerable to wildfire-related disturbance (Benda et al. 1998; Montgomery 1999; Dwire and Kauffman 2003). These streams also contain rainbow trout *Oncorhynchus mykiss*. Rainbow trout are an ideal study organism because their biology is relatively well understood, and salmonids in general have been shown to be plastic and diverse in their responses to changing environmental conditions (Quinn 2005).

To select headwater streams for sampling within the Middle and North Fork Boise River Basin in 2003, we restricted our sampling frame to streams that drained watersheds in area from 1000-5300 ha. For streams within this range, we segregated them into three disturbance categories: streams without stand-replacing wildfire in the last century (hereafter, unburned), streams that experienced stand-replacing wildfire prior to our study (hereafter, burned), and streams with stand-replacing wildfire followed by massive channel reorganization resulting from debris flows or severe floods prior to our study (hereafter, burned and reorganized). Because we were interested in lasting effects of wildfire and channel disturbance rather than the immediate effects, streams that had experienced severe wildfire after 1994 were eliminated from the sampling frame. For all remaining headwater streams, we defined stream networks and stream segments using a geographic information system (GIS, ArcInfo Inc.) and 30 m resolution digital elevation maps (DEMs) using the TauDEM software package (Tarboton 1997; 2004). Tributary junctions defined stream segments, and characteristics of the segments were estimated from DEMs, including stream channel slope (%), contributing area (ha), and elevation (m) at the downstream end. We used visual inspection of scatter plots based on these raw data to select 9 similar headwater streams for sampling, 3 in each disturbance category (unburned, burned, and burned and reorganized), with overlapping elevations, slopes, and contributing areas (For more detail on site elevation and temperature characteristics, see Dunham et al. 2007).

According to records maintained by the Boise National Forest, streams we considered unburned had not experienced wildfire over the past century (Lost Man and Beaver creeks) or had a watershed that was only lightly burned and had little evidence of wildfire a decade after the event (Trail Creek). Streams included in our burned category experienced stand-replacing burns throughout most of their catchments (Cottonwood, Hungarian, and Lost creeks). In burned and reorganized streams (South Fork Sheep, Trapper, and Wren creeks), stand-replacing wildfires were followed by small, isolated thunderstorms that triggered massive channel-reorganizing debris flows and

hyperconcentrated floods (Benda et al. 2003; for photographs of streams representing these disturbance types see Dunham et al. 2007).

Studies conducted in the summer of 2003 established that stream temperatures in the wildfire-affected streams were significantly warmer in the summer months than unaffected streams a decade after wildfire, particularly in those streams affected by both wildfire and channel reorganization (Dunham et al. 2007; Figure 3.3.I 2). In contrast, streams affected by wildfire were colder during the winter months than unburned streams (J. Dunham, unpublished data; Figure 3.3.I 2). In addition, in this system, warmer streams affected by wildfire can be characterized by a macroinvertebrate food base in the summer months that has less diversity, aquatic individuals that are smaller in size, and less terrestrial input during the fall months, all of which suggest a potential cost in terms of food availability for resident rainbow trout in these streams (Rosenberger et al. unpublished data). These disturbance-driven environmental changes may have a variety of important effects on growth and survival of rainbow trout that could translate into a variety of measurable responses at the level of individuals or populations.

Rainbow trout distribution and abundance

In each of the nine streams selected for sampling, 10 sample sites were randomly located within stream segments nested at progressively smaller catchments to a minimum of 400 ha (Figure 3.3.I 1). This allowed sampling of longitudinal gradients in these streams while maintaining randomness in site selection. We focused on segments with watersheds larger than 400 ha because they were more likely to support perennial surface flow in this system. During the summer of 2003, we completed 4-pass electrofishing using a backpack electrofisher (12B electrofisher, Smith Root, Vancouver, WA) in closed sites that were approximately 100 m in length. Blocknets with a 7mm diameter mesh were used to close the sites. All captured fish were identified to species, anaesthetized with tricaine methosulfonate (MS 222) and measured for fork length (FL).

From these data, we calculated the abundance of rainbow trout in each site. A validation study examining habitat correlates of rainbow trout sampling efficiency has been conducted previously in the Boise River Basin for streams with overlapping habitat characteristics (Rosenberger and Dunham 2005). This study contains models of rainbow trout sampling efficiency that can be used to correct 4-pass cumulative catch of rainbow trout >60mm to more realistically reflect actual numbers of rainbow trout present in the sites (Rosenberger and Dunham 2005). Fast growth of young-of-year (YOY) rainbow trout in our study streams over the summer may have contributed to YOY recruitment into the sampled population >60mm. Interpretation of length-frequency histograms generated for each stream (all sites combined) allowed us to identify and eliminate small individuals likely to be YOY from cumulative catch numbers that were then used to obtain abundance estimates of rainbow trout 1 y of age or older using methods described above. With measurements of average stream width and the total length of stream sampled, we converted corrected rainbow trout abundances to densities of rainbow trout (number of fish per m^2 stream area).

Individual characteristics of rainbow trout
In early October of 2003, 20 rainbow trout over a range of sizes (57-178mm FL) were collected from each of the 9 streams for analysis of lipid contents prior to the onset of winter (N = 180 rainbow trout). Sampling for these fish was conducted in an upstream direction with a single backpack electrofishing pass. Sampling began 300m upstream from the confluence of the stream with the Middle or North forks of the Boise River, with the exception of Cottonwood Creek. A significant length of stream upstream of the mouth of Cottonwood Creek was unburned or only lightly burned; therefore, fish sampling began approximately 300 m upstream of the downstream extent of the severe burn in this system. Rainbow trout selected for this study were euthanized with MS22, measured, weighed, and dissected to remove stomach contents and to note maturity. If the individual was mature, sex was notedl. After tagging, individuals were immediately frozen in the field using dry ice. Frozen specimens were then sent to a food laboratory for lipid content analysis (% dry weight).

In late September of 2004, we revisited a subset of the nine streams to collect information on growth and maturity of individual rainbow trout prior to winter and the spring spawning season. Cottonwood (burned) and South Fork Sheep (burned and disturbed) creeks were omitted due to logistic and time constraints. As with the lipid analysis, sampling began 300m upstream from the stream confluence and proceeded upstream with a single pass. Fish were collected, anaesthetized with MS222, measured, and classified as immature, mature male, or mature female. To avoid excessive mortality of rainbow trout, data on fish maturity and sex were obtained using two approaches: 1) fish were euthanized with MS 2222 and dissected for visual determination of maturity and sex or 2) fish were anaesthetized and an endoscope was used for internal visualization of sex organs to determine maturity and sex (Richard Wolf® 25 degree, Panoview Plus endoscope with a battery-powered fiber optic light source WelchAllyn Solarc Light Source® LB-21). The endoscope is a useful and accurate non-lethal approach for obtaining information on fish maturity and sex for trout (Swenson et al. in press). The primary source of error using this technique is occasional misclassification of immature individuals or mature females as mature males (error rate = 5%); visceral fat can be mistaken for testes using this technique (Swenson et al. in press). To eliminate this source of error, individuals determined to be mature males through the endoscope were euthanized with anesthetic and dissected to visually verify the endoscope diagnosis.

To obtain information on fish age, otoliths and scales were collected from euthanized individuals, and scales were obtained from individuals released after endoscopy (Murphy and Willis 1996). The accuracy of ageing using scales was verified through comparison with otoliths. Otoliths and scales were scored independently by two observers using a dissecting microscope and lateral light source. In the case of disagreement, a third observer and consultation among the two previous observers was used to resolve discrepancies.

Analysis of field data
We summarized fish abundance in two ways: 1) abundance of individuals >60 mm FL and abundance of age 1 + individuals. We examined differences in site abundance of age

1 + disturbance histories through a fixed-effects ANOVA model by disturbance history (burned, unburned, and burned and reorganized) and stream (N = 9 streams, ten sites per stream) to represent interdependence of sites within the same stream Densities of fish greater than age 1 were log transformed to meet normality assumptions.

We lumped data from streams with a common disturbance history to examine differences among disturbance types in fish lipid content (% dry weight). We used a fixed-effects analysis of variance (ANOVA) model, with disturbance history and length (FL) of fish as fixed effects. For this analysis, Scheffe's multiple comparisons were used to examine differences among treatments.

For individual rainbow trout life history data collected in fall of 2004, we used analysis of variance (with age as a covariate and Scheffe's multiple comparisons) to examine differences among treatments in log-transformed length-at-age. We summarized maturity information for each disturbance history (streams combined) by age. We used a chi-square test for heterogeneity to look for differences among disturbance histories in % immature, mature male, and mature female by age (Age 0, 1+, and 2+). All statistical analyses were performed in the Statistical Analysis System (SAS 2002), with the exception of Chi-squared analyses calculated by hand.

Individual-Based Model

Analyses of field data summarized above revealed population- and individual-based differences among streams with different disturbance histories. To test hypotheses and identify mechanisms to explain observed patterns (e.g., differences among streams in summer and winter temperatures drive differences among stream types in fish abundances, growth, and timing of maturity), we used an individual based model, inSTREAM, whose general purpose is to predict how stream trout populations respond to variation in habitat variables such as flow, temperature, turbidity, channel slope, and cover availability. We used the model version 4.2 inSTREAM, documented fully by Railsback et al. (in prep; see also www.huboldt.edu/~ecomodel); other versions were documented and applied by Railsback and Harvey (2001, 2002), Railsback et al. (2003), and Railsback et al. (2005). This model represents how growth, survival, and reproductive success of individual trout are affected by habitat conditions and competition for food and the population characteristics that emerge from what happens to individuals. Our focus in using this model was on key differences among disturbance histories in stream temperatures, which could be imposed on an inSTREAM environment on model fish with approximate physiological characteristics and behaviors known for rainbow trout.

Model description

inSTREAM represents a stream reach as a collection of rectangular habitat cells, each with its own depth and velocity that vary with daily flow input. Cells also have variables representing field-observed availability of cover for hiding and feeding. A model trout's growth depends on the concentration of food items in the drift (assumed constant over time and space) and its cell's depth and velocity (which determine how much drift the fish encounters), the fish's swimming speed (determined by cell velocity and availability

of feeding cover and affecting metabolic energy consumption), and temperature (which affects metabolic rates). Competition among trout for food is modeled as a size-based hierarchy: fish have access only to the food in a cell that remains uneaten by larger fish in the cell.

The model represents several potential sources of mortality, but the most important are predation by other fish and predation by terrestrial predators (e.g., birds, mammals, and snakes that feed primarily, but not exclusively, by sight). Predation by fish is greatest for small individuals in deep habitat, while terrestrial predation is higher for large individuals in shallow depths and low velocities, where little hiding cover is available. In addition, fish that are unable to maintain positive growth face increasing risk of starvation mortality as their weight declines.

The primary adaptive behavior of model trout is habitat selection: each day, individuals select the habitat cell (within a radius that individuals are assumed familiar with) with the highest value of a fitness measure that reflects the benefits of both energy intake and survival probability (Railsback et al. 1999; Railsback and Harvey 2002). Typically, this behavior causes fish to select the cell that provides highest survival probability among those that also provide positive growth.

Several effects of water temperature are represented in inSTREAM. Metabolic energy demands increase with temperature, so at higher temperatures fish require more food and must use riskier habitat to obtain it, balancing the additional predation risk against starvation risk. At very low temperatures, daily food intake is limited to low levels to reflect low gut passage rates. Spawning can only occur when temperatures are within a range (here, 4.5–13°C) where spawning has been observed in real trout. Incubating trout eggs are increasingly subject to disease mortality as temperatures exceed 10°. Finally, eggs incubate more rapidly at higher temperature, so increased temperature causes eggs to hatch into new trout earlier in the summer.

Spawning behavior is represented simply. The criteria for when females are ready to spawn include a (1) length-based stochastic function discussed below, (2) a weight threshold of 98% of normal for their length, (3) a date window (April–June in this case), (4) temperature within the allowable range, and (5) relatively steady flow. On days when these criteria are met, whether spawning actually occurs is a stochastic event with a probability of 0.04 (which spreads spawning out through the date window and provides an 84% probability of spawning within 30 suitable days). Model trout have no ability to adapt their decision of when to spawn, or at what size or age to spawn, either genetically or behaviorally.

Model modifications

Because inSTREAM is extensively documented and tested elsewhere, for the purposes of this manuscript, we focus mainly on modifications to the program relevant to testing hypotheses and mechanisms related to rainbow trout response to disturbance.

Our objective in using inSTREAM was to analyze the extent to which differences in water temperature explained observed differences in rainbow trout population and individual characteristics among streams with different disturbance histories. To do this, we developed a temperature input (daily mean water temperature, for the full year) to represent differences among unburned, burned, and burned and reorganized streams (Figure 3.3.I 2). We then executed inSTREAM for the three scenarios with temperature input as the only difference among these scenarios. We then examine the resulting differences in the simulated trout populations to determine the extent to which they reproduced the observed patterns of difference among site types. Model results were also examined in detail to identify the specific temperature-driven mechanisms that produced the differences among site types.

Temperature input to represent the three scenarios were developed from field data collected at Boise basin sites in the nine streams from which field data were collected (Figure 3.3.I 2). Temperature loggers were located in sites of similar elevation and stream size from mid-June through mid-October 2003, producing three records for each disturbance history. These values were averaged within disturbance history to produce daily summer temperatures typical of each disturbance history. During winter, temperatures were monitored at only one site of each type: Beaver (unburned), Lost (burned), and Trapper (burned and disturbed) creeks. The values were combined to produce a one-year temperature record that was used for all the simulated years. No data were available for September 2 through October 9 and for June 9 through July 1; these gaps were filled simply via linear interpolation between the values at their start and end.

Model simulations

Trout were simulated in the inSTREAM environment over 10 consecutive years. All of the years were identical in terms of flow and temperature input. For analysis, we eliminated results from the first five years to minimize the effects of initial input to the trout population (numbers in each age class). We obtained one mid-October "census" (one day's model output) per simulated year, and averaged the five annual census values to obtain mean results per model run. Because of the multiple random elements to the model, we executed five replicates of the model runs, all of which had slightly different outcomes. The mean and standard error over the five replicates of the results represent the central tendency and variation among replicates due to model stochasticity, not variation in simulated trout populations over time or variation among individuals (This standard error is not comparable to any field data analysis results).

Analysis of IBM output

The purpose of the inSTREAM model is not used in this case to directly predict or reproduce absolute numbers off fish or growth of individual fish for each stream disturbance type, but rather is used to see if specific observed differences in their environment (e.g., temperature) result in similar differences among stream types in abundance, growth, and maturity. Similarly, variation in the data results from random components of the model rather than actual variability observed in the field. Therefore, we do not use statistical analysis to examine differences among temperature scenerios, but rather examine the relative differences among scenarios to see if overall patterns

match our field observations. Based on a mid-October census of the data, we report Age 0+, Age 1+, and Age 2+ abundance, length, and the fraction that are mature.

Results

Rainbow trout distribution and abundance

Rainbow trout were present in all study streams, regardless of disturbance history, and found in all sites from the headwaters to the mouths of these streams (Table 3.3.I 1). Validated abundance estimates of fish > 60 mm, the length at which fish are recruited to electrofishing sampling gear, show significant overlap in fish abundances among streams with different disturbance histories; however, examination of length frequency histograms indicate that YOY fish were recruiting to the sampling gear. YOY recruitment was greatest for streams sampled later in the growing season; however, YOY recruitment was particularly strong in warmer, wildfire-affected streams, particularly burned and disturbed streams (Figure 3.3.I 3). Highest densities of fish greater than 1 year of age were found in unburned streams, and the lowest densities of fish were found in streams that experienced both wildfire and channel disturbance (Table 3.3.I 1; Figure 3.3.I 3). If density estimates were restricted to those fish likely to be age 1 or older based on interpretation of length-frequency histograms (Figure 3.3.I 3), there was a significant effect of stream disturbance history on fish densities when interdependence of sites within streams were taken into account (Table 3.3.I 1; General Linear Model, $F = 20.3$, $P < 0.001$ $df = 8$, multiple $R = 0.67$; disturbance history $F = 67.45$, $P < 0.001$, $df = 2$; Stream effect, $F = 4.57$, $P = 0.005$, $df = 6$).

Individual characteristics of rainbow trout

Lipid content of rainbow trout captured in autumn of 2003 in our study streams was significantly related to the disturbance history of the stream of origin and positively related to fish fork length (General Linear Model $F = 14.11$, $P < 0.001$, $R = 0.49$, $df = 4$; disturbance history [class variable] $F = 17.0$, $P < 0.001$, $df = 2$; Fork length $F = 15.7$, $P < 0.001$, $df = 1$). Multiple comparisons show that rainbow trout in burned and disturbed streams had lower lipid content than the other two disturbance types (Least Significant Means unburned = 4.67, burned = 4.97, burned and reorganized = 4.23). Fish in burned and reorganized streams had significantly lower lipid content than burned streams ($P = 0.002$) and marginally lower lipid content than in unburned streams ($P = 0.07$).

Fish sampled in our study streams in the autumn of 2004 were primarily age 0+ and 1 + individuals (Figure 3.3.I 4a). Older individuals were more frequently captured in unburned streams than the other two stream types (unburned N Age 2+ = 19, 3+ = 6, 4 + = 1; burned N Age 2+ = 8; 3+ = 0, 4+ = 0; burned and reorganized N Age 2+ = 8, 3+ = 1, 4 + = 0). The disturbance history of the stream had a significant effect on log-transformed length at age for Age 0+ to 2+ individuals (General Linear Model $F = 204.04$, $P < 0.001$, $R = 0.82$, $df = 4$; disturbance history $F = 116.7$, $P < 0.001$, $df = 2$; Age $F = 376.5$, $P < 0.001$, $df = 2$). Trout in warmer, burned and reorganized streams grew the most quickly, and trout in cooler, unburned streams grew the slowest (Figure 3.3.I 4; Scheffe multiple comparisons, $P < 0.001$).

Faster growth of trout in warmer, burned and burned and reorganized streams corresponded with earlier onset of maturity (Figure 3.3.I 4b). Most Age 0+ individuals were immature, and there was no significant difference among disturbance types in the proportion of individuals in maturity categories ($\chi^2 = 2.9$, $P = 0.23$). However, although all Age 0+ individuals in unburned streams were immature, we observed a low incidence of mature males of this age in all streams with a history of wildfire and, remarkably, one Age 0+ mature female in a burned and reorganized stream (Figure 3.3.I 4b). Differences among disturbance types in onset of maturity are most dramatic for Age 1+ individuals (Figure 3.3.I 4b; $\chi^2 = 70.7$, $P < 0.001$). Whereas most Age 1+ individuals in unburned streams are immature with low incidence of mature males, in burned streams, mature males were frequently observed in the 1+ age group. In addition, in burned and reorganized streams, 17% of Age 1+ individuals were females that were mature for the following spring spawning season. Sample sizes of Age 2 + individuals were small, particularly for burned streams, and differences among disturbance types in proportions of individuals in different maturity categories were minor and not statistically significant (Figure 3.3.I 4b; $\chi^2 = 1.6$, $P = 0.45$).

Individual Based Model

Simulations of the unburned, burned, and burned and reorganized stream temperature regimes in the inSTREAM environment for trout reproduce the pattern of fish abundance that we observed in the field results (Figure 3.3.I 4). Simulations with the burned and reorganized temperature regime had the lowest abundances of trout for each age class, and the simulations with the temperature regime of an unburned stream had the highest abundances (Figure 3.3.I 4). We were unable to determine if differences among simulated temperature scenarios in Age 0+ abundance matched field observations due to poor recruitment of small individuals (< 60mm FL) into our sampling gear (Figure 3.3.I 3).

Closer examination of model simulations suggest that poor bioenergetics conditions provided by the more extreme temperatures in burned and burned and reorganized streams is the most likely explanation for differences in fish abundances. During winter, temperatures are too cold in disturbed streams for food intake based on inSTREAM's function for maximum daily intake. During summer, the higher temperatures increase energy losses to metabolism, which directly subtracts from energy available for growth. Hence, trout in burned and, especially, burned and reorganized streams, lose more weight during winter and must occupy riskier habitat to obtain sufficient energy during warmer seasons. For all three scenarios and age classes, mortality was dominated by terrestrial predation and poor condition (starvation). These two mortality sources cannot be clearly separated because simulated trout make habitat selection decisions to balance starvation against predation risks. Temperature scenarios did affect survival of trout eggs; simulated mortality of eggs due to high temperature was 4%, 8%, and 11% for unburned, burned, and burned and reorganized streams, respectively. However, the loss of eggs was an unlikely cause of differences in trout abundances because most newly hatched fry perish during a period of density-dependent mortality in their first summer.

Despite this apparent similarity between inSTREAM simulations and field observations in fish abundance, the inSTREAM environment only partially reproduced observed patterns in fish growth and maturity. As was observed in field observations, Age 0+ individuals were greatest in length in simulations with burned and reorganized temperature regimes and smallest in unburned temperature regimes. However, these differences were small and did not persist to older age fish (Figure 3.3.I 6A).

Closer examination of the model suggests that the differences in growth in Age 0+ individuals among temperature regimes may be due to faster egg incubation in warmer temperatures. Fry emerge progressively earlier in the summer in warmer, disturbed streams and had more time to grow before the October growth census. These differences also may be due to the lower abundances of Age 0+ fish in warmer temperature simulations. Lower abundances means that fish have less competition for profitable feeding locations. Poor bioenergetic conditions in warmer scenerios is the likely explanation for why fish length in unburned temperature scenerios caught up with the wamer streams for older age classes.

inSTREAM results for sexual maturity show patterns resembling, but not completely, matching those for length. As in field observations, results show higher incidence of maturity of Age 0+ trout in burned and burned and reorganized streams (Figure 3.3.I 6B); however, unlike what was observed in the field, this did not continue to Age 1+ individuals. In fact, incidence of maturity in inSTREAM simulations was *lower* for burned and reorganized temperature scenarios than for burned and unburned scenarios. In the model, the probability of maturity varies steeply with trout length, and the relationship is especially nonlinear for the length range of Age 0+ trout, which explains the more dramatic difference among temperature scenarios in maturity than in length.

Conclusion Statement

For this study, we developed a series of hypotheses and predictions about responses of fish to disturbance, based on anticipated influences on growth, survival, and reproduction, given the environmental influences of wildfire, particularly temperature. We developed a series of hypotheses and predictions about responses of fish to disturbance, based on anticipated influences on growth, survival, and reproduction – given the environmental influences of wildfire. Our empirical observations of the responses of rainbow trout to disturbance were similar to other empirical studies of fish and invertebrate responses under similar conditions. Although responses observed were consistent with these other empirical datasets, we were not clear on the underlying mechanisms. We hoped that the IBM would reveal these mechanisms. We found that temperature partially, but did not entirely explain observed patterns.

References 3.2. II

Benda L, Miller D, Bigelow P, and Andras K. 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. Forest Ecology and Management 178:105-149.

Benda, L., D.Miller, T. Dunne, J. Agee, and G. Reeves 1998. Dynamic landscape systems. p261-288 In R. Naiman and R. Bilby, editors. River ecology and management: lessons from the Pacific Coastal Ecoregion. New York: Springer, New York.

Dwire KA, Kauffman JB. 2003. Fire and riparian ecosystems in landscapes of the western USA. Forest Ecology and Management 178:61–74.

Grimm, V. and S.F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, New Jersey.

Hendry, A.P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. Genetica 112-113:515-534.

Hendry, A.P., E.B. Taylor, and J.D. McPhail. 2002a. Adaptive divergence and the balance between selection and gene flow: lake and stream stickleback in the Misty system. Evolution 56:1199-1216.

Hilborn, R. and M. Mangel. 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, New Jersey.

Hilborn, R., T.P. Quinn, D.E. Schindler, and D.E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences 100:6564-6568.

Lytle, D.A. and N.L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19: 94-100.

Miller D, Luce C, Benda L. 2003 Time, space, and episodicity of physical disturbance in streams. Forest Ecology and Management 178:121-140.

Montgomery, D.R. 1999. Process domains and the river continuum. Journal of the American Water Resource Association 35:397-410.

Murphy, B.R., and D.W. Willis, editors. 1996. Fisheries techniques, second edition. American Fisheries Society, Bethesda, MD.

Quinn, T.P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. American Fisheries Society, Bethesda, Maryland; University of Washington Press, Seattle.

Railsback, S.F., 2001. Concepts from complex adaptive systems as a framework for individual-based modeling. Ecological Modelling 139:47-62.

Railsback, S. F., R. H. Lamberson, B. C. Harvey, and W. E. Duffy. 1999. Movement rules for spatially explicit individual-based models of stream fish. Ecological Modelling **123**:73-89.

Railsback, S., and B. Harvey. 2001. Individual-based model formulation for cutthroat trout, Little Jones Creek, California. General Technical Report PSW-GTR-182, Pacific Southwest Research Station, Forest Service, U. S. Department of Agriculture, Albany, CA.

Railsback, S. F., and B. C. Harvey. 2002. Analysis of habitat selection rules using an individual-based model. Ecology **83**:1817-1830.

Railsback, S. F., H. B. Stauffer, and B. C. Harvey. 2003. What can habitat preference models tell us? Tests using a virtual trout population. Ecological Applications **13**:1580-1594.

Railsback, S. F., B. C. Harvey, J. W. Hayse, and K. E. LaGory. 2005. Tests of theory for diel variation in salmonid feeding activity and habitat use. Ecology **86**:947-959.

Railsback, S. F., B. C. Harvey, S. K. Jackson, and R. H. Lamberson. in prep. inSTREAM: the individual-based stream trout research and environmental assessment model. USDA Forest Service, Pacific Southwest Research Station, Albany, California. Available at: www.humboldt.edu/~ecomodel.

SAS Institute. 2002. The SAS system for windows, version 9.1. SAS Institute, Cary, North Carolina.

Strand, E., Huse, G. and Giske, J. 2002. Artificial evolution of life history and behavior. American Naturalist 159:624-644.

Tarboton, D.G. 1997. A new method for the determination of flow directions and contributing areas in grid digital elevation models. Water Resources Research 33:309-319.

Tarboton, D.G. 2004. Terrain analysis using digital elevation models: a graphical user interface software package for the analysis of digital elevation data and mapping of channel networks and watersheds. Logan, UT: Utah State University.

Table 3.3.I 1. Densities of rainbow trout Age 1+ (# fish per m^2 stream area) based on validated per-site abundance estimates. Streams[1] for each disturbance type are ordered consecutively based on timing of sampling (early, mid, and late summer).

	Unburned			Burned			Burned and Reorganized		
Site/ Stream	BVR	TRL	LMN	CTW	HNG	LST	TRP	SFS	WRN
A	0.01	0.11	0.21	0.22	0.08	0.17	0.03	0.04	0.04
B	0.10	0.27	0.30	0.14	0.13	0.15	0.01	0.01	0.02
C	0.21	0.26	0.19	0.11	0.13	0.47	0.04	0.24	0.03
D	0.12	0.48	0.33	0.06	0.12	0.16	0.03	0.03	0.03
E	0.10	0.33	0.19	0.11	0.13	0.18	0.02	0.02	0.05
F	0.12	0.35	0.34	0.06	0.14	0.20	0.06	0.01	0.04
G	0.12	0.40	0.30	0.09	0.13	0.22	0.04	0.09	0.03
H	0.19	0.21	0.35	0.07	0.15	0.25	0.05	0.20	0.04
I	0.17	0.11	0.34	0.14	0.24	0.31	0.03	0.04	0.06
J	0.10	0.15	0.31	0.11	0.29	0.22	0.03	0.18	0.05

[1] BVR = Beaver, TRL = Trail, LMN = Lost Man, CTW = Cottonwood, HNG = Hungarian, LST = Lost, TRP = Trapper, SFS = South Fork Sheep, WRN = Wren

Figure Descriptions (3.3.I)

Figure 3.3.I 1. (omitted see Figure 3.2.I , closed circles) Map of the upper Boise River Basin, with shading to indicate3.2.I elevation and blue lines to represent stream and river systems. The primary river channels (North and Middle forks of the Boise River) and headwater streams selected for the field portion of this study are labeled, and closed circles represent locations where rainbow trout distribution and abundance data were collected. Wildfires occurring in different years are indicated by colored outlines around fire perimeters (black = 1992, white = 1994, green = 2000, purple = 2003). Red shading within outlines corresponds to fire severity (dark red = high severity; rose = intermediate severity; light pink = low severity). Spatial resolution of fire severity mapping was greatest for 2000 and 2003 wildfires.

Figure 3.3.I 2.
Year-long stream temperature input for the inSTREAM model representing differences among unburned, burned and burned and reorganized headwater streams. These scenarios are based on field data collected during the summer and winter months within headwater streams of the Boise River Basin, with the exception of 9/2 – 10/9 and 6/9 - 7/1, when data gaps were filled via linear interpolation.

Figure 3.3.I 3.
Length-frequency histograms of rainbow trout captured in 9 headwater streams[1] within the Boise River Basin. Ten separate sites per stream are combined to create a single histogram for each stream. Black bars represent fish likely to be older than 1 year of age based on interpretation of these histograms, and YOY are represented by white bars. Fish larger than 60mm FL to the right of the dotted line are dependably recruited to electrofishing sampling gear. Histograms are organized by disturbance type in rows (UB = unburned, BR = burned, RB = burned and reorganized) and by timing of sampling in columns (early to late summer).

Figure 3.3.I 4.
Life history data on fish captured in autumn of 2004 in headwater streams of the Boise River Basin. Data are presented by age class and were combined for each disturbance type (UB = unburned [black], BR = burned [white], RB = burned and reorganized [gray], followed by *N* parenthetically). (A) Box plots of length-at-age of fish captured in autumn. (B) Proportion of these fish in different maturity categories.

Figure 3.3.I 5
Abundance of (A) Age 0+ (white) and (B) Age 1+ (gray) and Age 2+ (black) trout in a simulated, individual-based modeling stream environment (census for October), where the only difference among simulations is temperature input (Figure 2), which represents differences in stream temperature among unburned (UB), burned (BR), and burned and reorganized (RB) headwater streams in the Boise River Basin. Error bars represent standard deviations around simulation means ($N = 5$). Note different scales on the two Y-axes.

Figure 3.3.I 6
Growth and maturity information for trout simulated in an individual based modeling stream environment, where the only difference among simulations is temperature input (Figure 2), which represents differences in stream temperature among unburned (UB), burned (BR), and burned and reorganized (RB) headwater streams in the Boise River Basin. (A) Length at age of simulated age classes based on October census. Error bars represent standard deviations around simulation means ($N = 5$). (B) % of individuals that are deemed mature according to the model.

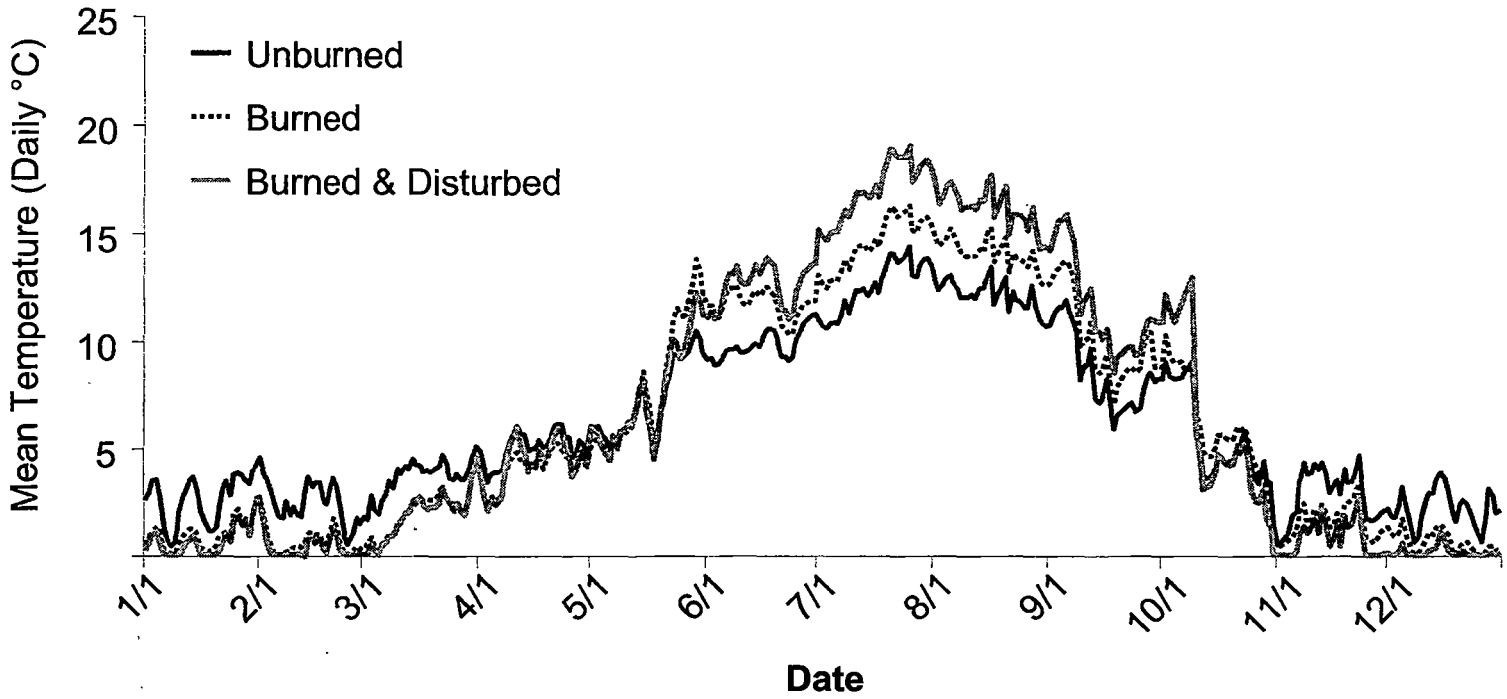

Mean Temperature (Daily °C)
25
20
15
10
5
Unburned
Burned
Burned & Disturbed
1/1
2/1
3/1
4/1
5/1
6/1
7/1
8/1
9/1
10/1
11/1
12/1
Date

Figure 3.3.I 2

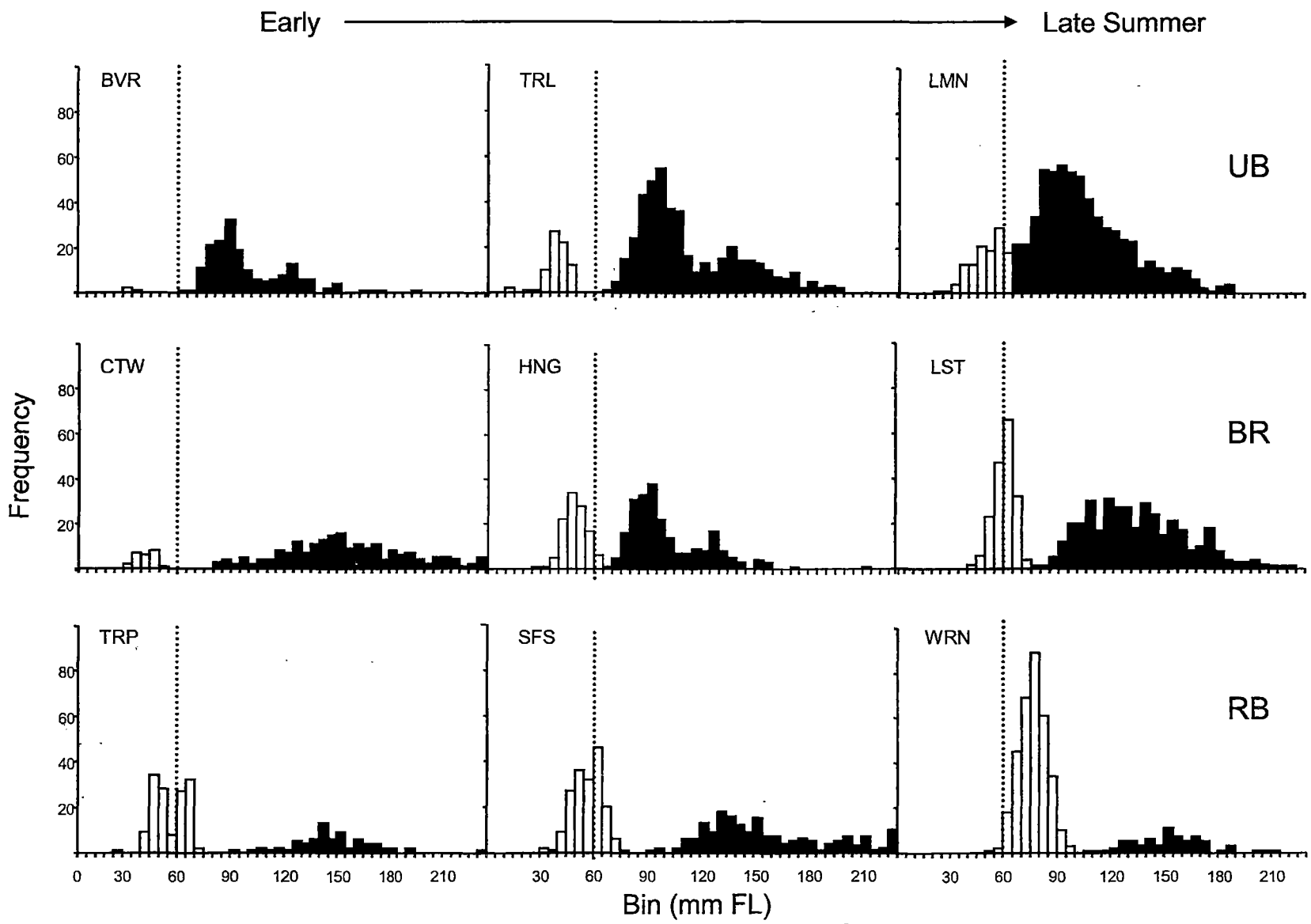

Early
Late Summer
BVR
TRL
LMN
UB
CTW
HNG
LST
BR
TRP
SFS
WRN
RB
Frequency
80
60
40
20
0
30
60
90
120
150
180
210
Bin (mm FL)

Figure 3.3.I 3

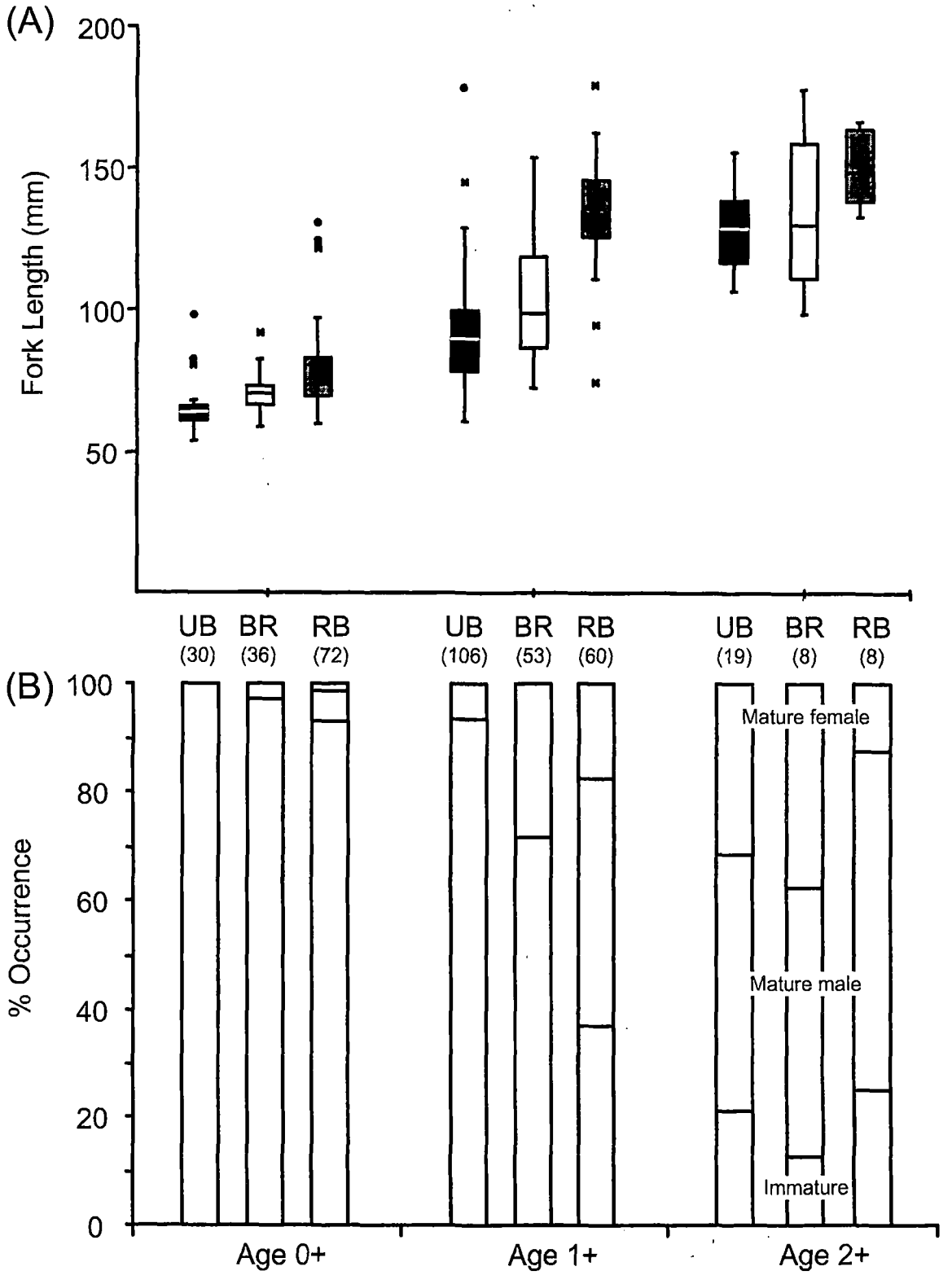
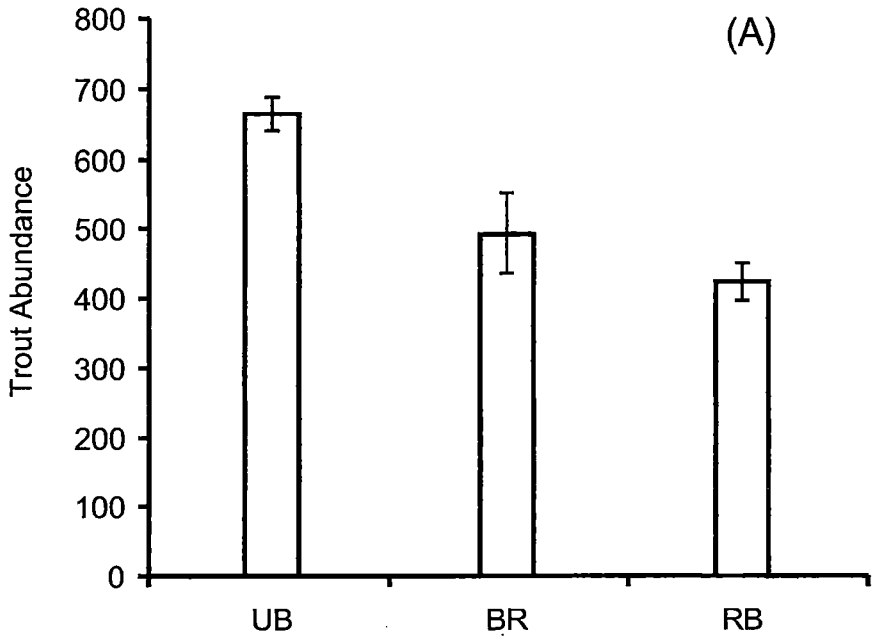

(A)
Fork Length (mm)
200
150
100
50
UB (30)
BR (36)
RB (72)
UB (106)
BR (53)
RB (60)
UB (19)
BR (8)
RB (8)
(B)
% Occurrence
100
80
60
40
20
0
Mature female
Mature male
Immature
Age 0+
Age 1+
Age 2+

Figure 3.3.I 4


(A)
Trout Abundance
800
700
600
500
400
300
200
100
0
UB
BR
RB

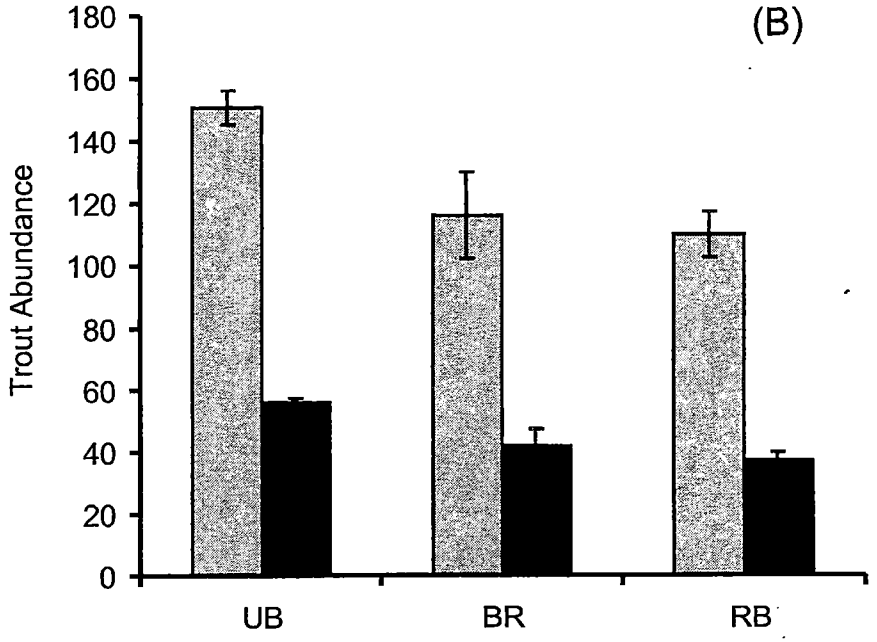

(B)
Trout Abundance
180
160
140
120
100
80
60
40
20
0
UB
BR
RB

Figure 3.3.I 5

GOAL 4: WORK WITH MANAGERS TO DEVELOP APPLICATIONS OF THESE RESULTS IN PRIORITIZATION OF FIRE MANAGEMENT ALTERNATIVES TO BENEFIT NATIVE AQUATIC VERTEBRATES AND TO DEAL EFFECTIVELY WITH NONNATIVE FISH INVASIONS.

We have disseminated the results summarized above widely (see Project Accomplishments section at the beginning of this report). All publications are available on the RMRS website. Tracking of website activity has documented over thousands of downloads and requests for papers.

Specific accomplishments

The Fire and Aquatic Ecosystems Workshop held April 22-24, 2002 in Boise, Idaho has also been extremely useful to managers. The purpose of the workshop was to synthesize new information and current knowledge of the role for fire in, and effects of fire on, aquatic and riparian ecosystems, and to explore potential research areas that will improve our understanding of these areas. The goal was provide a foundation for biologists and managers trying to protect and restore the ecosystems and important processes influenced by fire. The major organizing themes of the workshop were: fire history; vegetation and post-fire management; the effects of fire on physical and watershed-level processes; and the effects of fire on biological processes.

Fourteen papers were presented in the workshop. Over 30 leading scientists and managers authored thirteen peer-reviewed publications and a formal synthesis of fire management implications from the workshop. These papers appeared in a special issue of *Forest Ecology and Management*, published in June of 2003. Information on the workshop with links to related information and publications are available on the internet: www.fs.fed.us/rm/boise/teams/fisheries/fire/firehome.htm. Biologists and managers have utilized the workshop proceedings extensively.